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BIOCHEMISTRY OF PLANT DISEASES

V. RELATION BETWEEN SUSCEPTIBILITY TO BROWN ROT IN PLUMS AND PHYSICAL AND CHEMICAL PROPERTIES[1]

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(WITH TEN FIGURES)

An attempt is being made in these investigations to establish the fundamental explanation of differences in susceptibility to brown rot (*Sclerotinia cinerea*) in plum varieties. In previous articles in this series (**13**, **14**) it was reported that, although resistant and susceptible plum varieties differed in respect to density of juice, hydrogen ion concentration, titre, oxalic acid, ash, nitrogen, CaO, and ether extract content, the differences were hardly of sufficient magnitude to be related to the resistance properties. The crude fiber content, however, was conspicuously higher in the two resistant than in the two susceptible varieties. This suggested a physical difference in the texture of the fruit as the basis of the resistance properties. This hypothesis was worked on during the seasons of 1922 and 1923, therefore, and the results are reported in the following paper.

Previous work

Mechanical resistance on the part of a plant to the entrance of a fungus has been recognized by pathologists for some time as an

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important means of protection against disease. In 1892 COBB (1) found that certain wheats resistant to rust had thicker leaves, and these leaves had a thicker cuticle, more sclerenchymatous tissue, and greater tensile strength than wheats susceptible to the rust. Later, MELHUS, DURRELL, and KIRBY (9) noted that only the young leaves of the barberry were infected with rust, because the cuticle and epidermis of the older leaves were too thick for the entrance of the rust hyphae. MELANDER (8) actually measured the force required to puncture the young and old leaves of various species of barberry, and found a close relation between resistance and toughness of the leaves.

In 1915 VALLEAU (11) found that those varieties of plums having a thick and tough skin were most resistant to brown rot. He tabulated observations on skin properties and resistance of many different varieties. He also believed that firmness of the flesh, especially at ripeness, played a part in resistance. He made no direct measurements, however, of the force required to penetrate either the skin or the flesh of plums.

So far as the writers are aware, MORRIS of the Washington Agricultural Experiment Station was the first to use a mechanical pressure test on fruits. LEWIS, MURNEEK, and CATE (7) describe an apparatus, the idea for which they obtained from MORRIS. The latter used it to follow the changes in apples during storage, and the former the changes in pears during ripening.

The most accurate instrument for mechanical puncture tests is a modified Jolly balance, the delicate spring and vernier scales of which can readily be adapted for measuring the force necessary for various needles to puncture given tissues. Such an instrument was used by HAWKINS and HARVEY (3), HAWKINS and SANDO (4), MELANDER (8), and by the present writers in the work here reported. HAWKINS and HARVEY found that the reason McCORMICK potato tubers are more resistant to attack by *Pythium debaryanum* than are those of Green Mountain and Bliss Triumph is that the tissue is firmer, and resists in a mechanical way penetration by the fungus. Associated with the firmer texture is a markedly greater crude fiber content. After careful consideration of all observable evidence, these writers concluded that mechanical puncture is the only means this

fungus has of penetrating cell walls; and the mechanical measure of the hardness of the tissues thus becomes of real value. Furthermore, the osmotic pressure of the fungus hyphae was greater than that required to puncture the susceptible tubers, but less than that to puncture the resistant ones.

HAWKINS and SANDO were interested in explaining why small fruits kept in cool storage were less liable to spoilage than those kept at higher temperatures. They found that the average pressure required to puncture cool fruit was greater than that required for warm fruit. This held for strawberries, black raspberries, red raspberries, blackberries, and cherries. Thus the greater toughness of the skin is probably one of the factors in the better keeping of these fruits at lower temperatures.

Since previous work with plums by the present writers had shown that the resistant varieties were higher in crude fiber, it was decided to make a more extensive study of this factor, as well as of the mechanical properties of plum fruits. Eleven varieties of plums were used, covering the whole range of relative susceptibility to brown rot. Crude fiber, pentosan, dry matter, toughness of the skin, and firmness of the flesh were the factors measured.

Methods and apparatus

Crude fiber was determined by the Kennedy modification of the Sweeney method (**6**). Pentosans were determined by the method of PERVIER and GORTNER (**10**). Dry matter was determined by drying in an oven at 100° C. at atmospheric pressure. For the purpose at hand it was considered unnecessary to use any more careful method.

The toughness of the skin was measured by the apparatus shown in fig. 1. After a number of preliminary tests with glass and steel needles, it was decided to use the phonograph needles called "Sonora soft-tone," because of their uniform size, rounded point, and ease of accurate duplication. The needle was sealed into the bottom end of a 10 cc. pipette, cut off within an inch of the bulb. The pipette was filled with mercury until its weight was 40 gm., which was in excess of that required to puncture the toughest plum skin. A wire loop was then sealed into the upper end of the pipette, and the whole suspended from the spring of the balance. To make a determination,

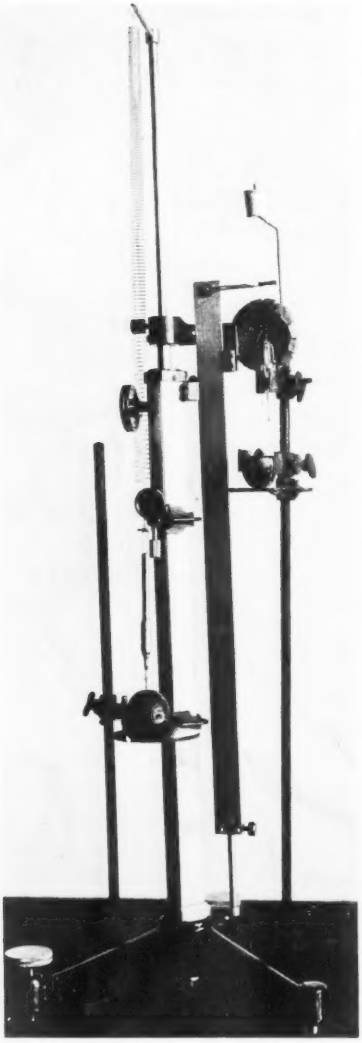

FIG. 1.—Jolly balance adapted for measuring force required to puncture skin and penetrate flesh of plum fruits.

the needle was suspended free on the spring, and the latter lowered until the point of the needle just rested on the surface of the plum, which was held in position on the stand by a clamp. The scale reading was then recorded. The weight of the needle was gradually placed on the plum by releasing the tension of the spring by means of the milled head. At the moment when the needle was observed to break through the skin, the lowering of the spring was stopped and the scale read again. The difference between the two readings indicated the relative amount of force required to press the needle through the skin of the fruit. This force has been recorded directly in centimeters for the sake of simplicity. By the use of the factor 0.9, the readings can be converted into grams, although no useful purpose would be served. Five or six plums of each lot were used, and each plum was tested three times at various points, avoiding the suture. Thus the recorded values are the average of fifteen or eighteen readings. Very concordant values were almost always obtained.

The penetration of the tissue was measured by a harpoon device on the other scale of the Jolly balance. The harpoon consisted of a piece of glass rod, with a no. 10 steel sewing needle fused in one end and a wire hook in the other. The needle was broken off squarely just above the taper, and the broken surface ground smooth, with rounded edges. The needle weighed 3.7067 gm. It was suspended by a thread in front of a small mirror fastened to the scale of the instrument. A few trials showed the approximate height from which the harpoon should be dropped into the plum; this height was marked on the mirror by two horizontal scratches, 18.7 mm. apart. To take a reading, the top point of the harpoon was sighted against the lower mark on the mirror; the plum to be tested was fixed in position so that the surface to be speared was just touching the harpoon; the scale reading was taken; the harpoon was raised until its top was sighted against the upper mark on the mirror; the thread suspending the harpoon was burned; the scale and mirror were lowered until the top of the harpoon again was sighted against the lower mark; the reading was taken, and the difference between the two readings represented the distance the harpoon had penetrated the tissue. A penetration reading as recorded here can thus be defined as the depth in centimeters that a harpoon weighing 3.7067 gm., pointed with a steel needle as described, and falling from a height of 18.7 mm., will penetrate the freshly cut surface of the flesh of the fruit. The harpoon fell through a short collar of glass tubing, which prevented its falling to one side. The plum to be tested was prepared as shown in fig. 2, the cutting being done with a sectioning razor, and every care being taken not to bruise the tissue. Each plum was usually tested twice on each side of the pit, and five plums in each lot were used. Thus the recorded readings are the averages of from fifteen to twenty determinations.

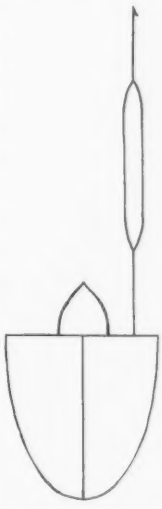

FIG. 2.—Sketch showing method of preparing plum for harpoon test, and position of harpoon when entering tissue.

Materials

Eleven varieties of plums were selected, grown at the University of Minnesota Fruit Breeding Farm at Excelsior,[2] and representing all degrees of susceptibility to brown rot. The values for the relative resistance assigned by VALLEAU were used. The plums were picked at six stages of maturity: the first stage was when the fruit was wholly green, but just showing signs of incipient yellowing; the fifth was when the plums were ripe for picking; the sixth when they were "dead" ripe; and the second, third, and fourth stages were judged arbitrarily by color. In 1922, several samples were unavoidably missed, but in 1923 a complete set was obtained.

Experimental results

The data obtained in 1922 are displayed in table I, and those in 1923 in table II. The varieties are listed in decreasing order of resistance, the plus signs indicating VALLEAU's ratings. In order to show the comparative values of the figures graphically, charts were constructed (figs. 3–10). The titles indicate the two methods of grouping the data, so that varieties may be compared at each stage of ripeness, and so that the progress of ripeness within each variety may be followed.

In scanning the charts, it should be remembered that the aim is to show the relation between varieties and their resistance to brown rot. For example, it was previously hypothecated, on the basis of work on potatoes and wheat, that in plums also the structural elements, the toughness of the skin, and the firmness of the tissue would be greatest in the resistant and least in the susceptible varieties. Since the varieties are arranged in order of decreasing resistance, the heights of the columns in the chart should tend to decrease from left to right, except in the case of the penetration data, where the softer tissues give the greater values.

In figs. 3 and 7 the percentage of dry matter bears no apparent relation to resistance properties. The crude fiber, however, has an unmistakable tendency to be higher in the resistant varieties. This is more marked in the later stages of ripeness. It is significant that

[2] The writers wish to acknowledge the kind assistance of Dr. J. H. BEAUMONT in selecting the varieties and in aiding in the collection of the samples.

these stages are the critical ones for brown rot, since infection seldom takes place in any variety during the very green stages (**2**). The crude fiber of each variety also decreases as ripeness proceeds (fig. 8), and this is more marked in the susceptible varieties. An exception to this tendency is noticed in many of the "dead" ripe samples (stage VI), where the fiber suddenly increases. This is probably due to the loss of sugars by combustion, and the consequent relative increase of the inert crude fiber.

HAWKINS and HARVEY estimated the pentosan content of potato tubers, to determine whether it as well as the crude fiber contributed to the resistance properties of the tubers. They could find no such relation, however, in the three varieties they tested. The 1922 lots of plums were analyzed for pentosans, with the results shown in fig. 4. There is some evidence of more pentosans in the resistant varieties, and of less in the riper stages; but these tendencies are not so marked as in the case of the crude fiber. Since both of these substances contribute to the structural elements of plant tissues, justification was felt for combining the two values, especially since a test showed that the crude fiber contained no appreciable amount of pentosan. This was done in fig. 5. It is obvious that the varietal differences are enhanced, indicating still more convincingly that the cell wall materials of these fruits play an important part in their resistance to brown rot.

The toughness of the skin of all varieties decreases considerably in the last three stages of ripeness, as the puncture values in figs. 6, 9, and 10 indicate. Furthermore, it decreases more in the susceptible than in the resistant varieties. The differences are marked and very consistent. Also, as would be expected, the tissues become softer as the fruit ripens, and this is more marked in the susceptible varieties. It will be noted that the limiting value of penetration is 3.0 cm. This value was arbitrarily assigned to a sample when the harpoon buried itself to the "hilt," or when the point protruded through the plum, so that perhaps some of these values should be somewhat greater than 3.0 cm. The plums of two resistant varieties, Burbank×Wolf 15 and 9 (fig. 9), in stage VI became as soft as the susceptible, indicating further why differential resistance among varieties tends to disappear as ripening becomes far advanced.

TABLE I

ANALYSES OF PLUM VARIETIES, SEASON OF 1922, LISTED IN ORDER OF DECREASING RESISTANCE TO BROWN ROT

LABORATORY NO.	DATE PICKED	STAGE OF RIPENESS	PUNCTURE (CM.)	PENETRATION (MM.)	DRY MATTER (PER CENT)	CRUDE FIBER (PER CENT)		PENTOSANS (PER CENT)		PENTOSANS+CRUDE FIBER (PER CENT)	
						Wet basis	Dry basis	Wet basis	Dry basis	Wet basis	Dry basis
	Burbank×Wolf 15 (15) +*										
16	August 8	1	21.0	0.30	11.68	0.97	8.30	0.67	5.74	1.64	14.04
31†	August 20	3	23.8	0.50	8.80	1.05	11.93	0.50	5.68	1.55	17.61
32	August 20	4	22.3	0.54	10.71	0.91	8.50	0.50	4.67	1.41	13.07
41†	September 4	6	17.4	1.45	8.76	0.99	11.30	0.47	5.37	1.46	16.67
	Abundance×Wolf 18 (18) +*										
6	August 2	2	21.6	0.22	11.11	1.12	10.08	0.75	6.75	1.87	16.83
30	August 16	3	22.5	0.40	13.00	1.01	7.77	0.73	5.62	1.74	13.39
36	August 28	5	22.0	0.78	14.90	1.03	6.91	0.60	4.03	1.63	10.94
	Burbank×Wolf 9 (9) +*										
2	July 18	1	.....	0.23	.....	.....	.....	.....	.....	.....	.....
5	August 2	2	21.6	0.29	10.52	0.81	7.70	0.67	6.36	1.48	14.06
27	August 16	3	25.2	0.51	12.17	0.71	5.83	0.52	4.27	1.23	10.10
37	August 28	4	20.8	1.00	12.18	0.68	5.58	0.43	3.53	1.11	9.11
38	August 28	5	18.7	1.14	12.14	0.59	4.86	0.46	3.79	1.05	8.65
42	September 4	6	18.6	1.25	12.91	0.54	4.18	.....	.....	.....	.....
	Burbank×Wolf 12 (12) ++*										
14	August 4	2	26.3	0.34	10.59	0.81	7.65	0.54	5.10	1.35	12.75
19	August 10	3	20.4	0.59	10.79	0.67	6.21	0.55	5.10	1.22	11.31
29	August 16	4	16.8	0.92	11.77	0.68	5.78	0.46	3.91	1.14	9.69

	Burbank×Wolf 21 (21) ++*										
3	July 28	1	25.3	0.41	11.24	0.68	6.05	.....	.....	.....	.....
12	August 4	2	26.8	0.53	11.56	0.94	8.13	0.57	4.93	1.51	13.06
17	August 8	3	23.6	0.60	13.60	0.90	6.62	0.49	3.60	1.39	10.22
20	August 10	4	25.4	0.74	11.96	1.10	9.20	0.45	3.76	1.55	12.96
24	August 14	5	19.4	0.77	12.23	0.76	6.21	0.45	3.68	1.21	9.89
33	August 20	6	13.2	1.53	11.27	0.69	6.12	0.44	3.90	1.13	10.02
	Burbank×Wolf 16 (16) ++*										
15	August 8	1	27.2	0.35	11.27	0.74	6.57	0.55	4.88	1.29	11.45
	Assiniboine (As) +++*										
1	July 18	1	.....	0.27	.....	.....	.....	.....	.....	.....	.....
7	August 2	3	18.9	0.64	13.27	0.71	5.35	0.61	4.60	1.32	10.95
13	August 4	4	20.7	0.97	13.17	0.67	5.09	0.50	3.80	1.17	8.89
22	August 10	5	14.9	3.(ca.)	12.78	0.64	5.01	0.46	3.60	1.10	8.61
23	August 14	6	11.5	3.(ca.)	13.47	0.72	5.35	0.50	3.71	1.22	9.06
	Abundance×Wolf 30 (30) ++++*										
4	July 28	1	27.1	0.28	15.28	1.04	6.81	.....	.....	.....	.....
28	August 16	2	27.3	0.47	14.50	0.97	6.69	0.54	3.72	1.51	10.41
35	August 28	3	22.7	0.92	.....	.....	.....	0.46	.....	.....	.....
40	August 31	4	13.2	1.24	11.59	0.69	5.95	0.49	4.23	1.18	10.24
43	September 4	5	13.1	1.55	.....	.....	.....	0.40	.....	.....	.....
44†	September 4	6	14.8	1.76	10.79	0.48	4.45	0.47	4.36	0.95	8.81

* + = greatest relative resistance; ++++ = least relative resistance.
† Nos. 31, 41, and 44 were probably unfit specimens kept over several days without ice.

TABLE I—*Continued*

Laboratory no	Date picked	Stage of ripeness	Puncture (cm.)	Penetration (mm.)	Dry matter (per cent)	Crude fiber (per cent)		Pentosans (per cent)		Pentosans+crude fiber (per cent)	
						Wet basis	Dry basis	Wet basis	Dry basis	Wet basis	Dry basis
	Emerald (Em) ++++*										
21	August 10	1	29.6	0.29	13.68	0.89	6.51	0.65	4.75	1.54	11.26
34	August 20	2	26.4	0.50	13.62	0.74	5.43	0.62	4.55	1.36	9.98
39	August 31	3	22.7	0.98	12.44	0.59	4.74	0.56	4.50	1.15	9.24
45	September 13	5	18.2	1.49	15.14	0.59	3.90	0.51	3.37	1.10	7.27
46	September 13	6	16.3	3.(ca.)	14.33	0.50	3.49	0.51	3.56	1.01	7.05
	Sand cherries (SC) ++++*										
8	August 2	2	17.3	0.35	11.03	0.65	5.89	0.48	4.35	1.13	10.24
9	August 2	4	12.2	0.74	13.14	0.44	3.35	0.60	4.57	1.04	7.92
10	August 2	5	.....	3.(ca.)	13.68	0.38	2.78	0.54	3.95	0.92	6.73
18	August 8	6	4.2	.....	14.42	0.35	2.43	0.44	3.05	0.79	5.48
	Compass (C) ++++*										
11	August 4	3	20.4	0.66	12.68	0.65	5.13	0.64	5.05	1.29	10.18
25	August 14	5	15.1	3.(ca.)	12.98	0.60	4.62	0.35	2.70	0.95	7.32
26	August 14	6	11.5	3.(ca.)	13.93	0.41	2.94	0.47	3.37	0.88	6.31

TABLE II

ANALYSES OF PLUM VARIETIES, SEASON OF 1923, LISTED IN ORDER OF DECREASING RESISTANCE TO BROWN ROT

LABORATORY NO.	DATE PICKED	STAGE OF RIPENESS	PUNCTURE (CM.)	PENETRATION (MM.)	DRY MATTER (PER CENT)	CRUDE FIBER (PER CENT)	
						Wet basis	Dry basis
	Burbank×Wolf 15 (15) +*						
19	August 9	1	21.3	0.31	10.98	0.61	5.52
31	August 18	2	17.2	0.51	10.88	0.54	4.97
37	August 21	3	17.1	0.66	10.36	0.48	4.63
46	August 25	4	15.0	0.69	10.28	0.51	4.94
53	August 28	5	12.4	1.07	10.46	0.49	4.68
60	September 8	6	8.4	3.(ca.)	9.89	0.84	8.50
	Abundance×Wolf 18 (18) +*						
15	August 7	1	23.0	0.27	10.89	0.96	8.81
30	August 18	2	17.7	0.44	13.05	0.73	5.59
45	August 25	3	16.2	0.54	14.20	0.50	3.52
55	September 1	4	14.0	0.71	13.39	0.64	4.76
61	September 8	5	12.7	1.39	14.94	0.68	4.52
64	September 14	6	11.4	1.26	14.51	0.66	4.57
	Burbank×Wolf 9 (9) +*						
25	August 9	1	21.8	0.32	11.33	0.77	6.80
21	August 9	2	21.0	0.37	12.24	0.69	5.64
38	August 21	3	20.3	0.55	13.02	0.49	3.73
44	August 25	4	15.1	0.95	12.58	0.46	3.67
52	August 28	5	11.4	1.40	12.00	0.49	4.11
59	September 8	6	7.7	3.(ca.)	11.25	0.52	4.60
	Burbank×Wolf 12 (12) ++*						
8	August 2	1	26.9	0.30	9.27	0.77	8.26
16	August 7	2	24.0	0.35	11.39	0.71	6.28
17	August 7	3	20.8	0.46	12.56	0.66	5.26
33	August 18	4	11.6	0.70	13.60	0.58	4.28
40	August 21	5	11.2	0.97	15.69	0.48	3.06
42	August 25	6	10.7	1.09	17.70	0.56	3.17
	Burbank×Wolf 21 (21) ++*						
1	July 28	1	24.5	0.45	12.01	0.63	5.28
9	August 4	2	22.2	0.52	13.79	0.50	3.63
10	August 4	3	22.1	0.62	14.38	0.52	3.64
23	August 9	4	16.1	0.60	13.78	0.44	3.18
27	August 14	5	15.4	0.81	13.26	0.39	2.94
39	August 21	6	10.9	1.08	13.65	0.42	3.07

* +=greatest relative resistance; ++++=least relative resistance

TABLE II—*Continued*

Laboratory no.	Date picked	Stage of ripeness	Puncture (cm.)	Penetration (mm.)	Dry matter (per cent)	Crude fiber (per cent)	
						Wet basis	Dry basis
	Burbank×Wolf 16 (16) ++*						
14.....	August 7	1	28.8	0.34	12.11	0.78	6.44
20.....	August 9	2	24.7	0.44	12.42	0.69	5.58
26.....	August 14	3	21.1	0.48	12.35	0.60	4.84
32.....	August 18	4	14.5	0.63	13.94	0.57	4.08
43.....	August 25	5	12.9	1.24	14.24	0.40	2.83
54.....	September 1	6	8.6	2.20	12.08	0.49	4.07
	Assiniboine (As) +++*						
2.....	July 28	1	23.5	0.31	10.59	0.86	8.12
7.....	August 2	2	20.5	0.45	11.96	0.72	6.00
13.....	August 4	3	18.8	0.55	12.21	0.80	6.53
22.....	August 9	4	14.0	1.35	11.46	0.46	4.02
28.....	August 14	5	9.3	3.(ca.)	11.71	0.47	4.00
34.....	August 18	6	7.2	3.(ca.)	10.54	0.48	4.58
	Abundance×Wolf 30 (30) ++++*						
35.....	August 18	1	20.5	0.43	14.76	0.56	3.79
49.....	August 25	2	17.4	0.75	14.59	0.55	3.73
50.....	August 25	3	16.3	0.76	13.89	0.57	4.09
56.....	September 1	4	11.0	1.05	14.07	0.49	3.50
62.....	September 8	5	8.9	3.(ca.)	14.40	0.46	3.22
65.....	September 14	6	7.6	3.(ca.)	13.16	0.50	3.78
	Emerald (Em) ++++*						
36.....	August 18	1	21.9	0.45	12.04	0.62	5.13
47.....	August 25	2	16.1	0.67	11.11	0.54	4.83
48.....	August 25	3	14.5	0.75	12.98	0.57	4.38
57.....	September 1	4	11.3	1.22	13.05	0.58	4.43
63.....	September 8	5	8.1	3.(ca.)	13.02	0.61	4.68
66.....	September 14	6	7.5	3.(ca.)	12.37	0.65	5.28
	Sand cherries (SC) ++++*						
3.....	July 28	1	17.6	0.37	7.35	0.75	10.12
4.....	August 2	2	18.5	0.44	8.39	0.71	8.40
18.....	August 7	3	15.8	0.54	7.97	0.62	7.74
29.....	August 14	4	11.4	3.(ca.)	8.72	0.38	4.34
41.....	August 21	5	7.7	3.(ca.)	9.51	0.32	3.41
58.....	September 1	6	4.9	3.(ca.)	9.99	0.38	3.80

TABLE II—*Continued*

Laboratory no.	Date picked	Stage of ripeness	Puncture (cm.)	Penetration (mm.)	Dry matter (per cent)	Crude fiber (per cent)	
						Wet basis	Dry basis
	Compass (C) ++++*						
5.....	August 2	1	20.1	0.35	10.74	0.67	6.25
6.....	August 2	2	15.6	0.66	10.03	0.57	5.67
11.....	August 4	3	13.1	0.83	11.23	0.43	3.80
12.....	August 4	4	12.2	1.23	10.36	0.44	4.20
24.....	August 9	5	10.5	3.(ca.)	9.40	0.36	3.81
51.....	August 25	6	5.2	3.(ca.)	13.53	0.35	2.58

The relation between the skin and the flesh texture of the plums can be shown in a different way graphically by plotting the two values against each other, and connecting the values of a single variety by a line. It is apparent that in general, as ripening proceeds, the flesh becomes softer and the skin tenderer; but that during the last stages the flesh softens far more rapidly than does the skin.

Since we are here obviously dealing with several correlated pairs of factors, it was thought desirable to find the mathematical value of these correlations. Because of the small number of samples involved, it was felt that the calculation of the standard coefficient of correlation was not justified; hence correlation by rank was calculated for the 1923 samples, using the formula given by JACKSON (**5**): $r = 1 - 6(\Sigma D_k^2)/(n^3 - n)$. The probable error was calculated by the following formula, taken from WHIPPLE (**12**): $e = 0.706 \times \frac{1 - r^2}{\sqrt{n}}$. The values for the factors of the eleven varieties for a given stage of maturity were used in the calculations. The results are given in table III.

Although in a way the group of individuals used in each case may be considered heterogeneous, because it consisted of numerous varieties instead of but one, it was felt that if, in spite of this, coefficients of some magnitude did appear, they would certainly be significant. Furthermore, the signs of the coefficients for a series would perhaps in themselves have a meaning. Because n is only 11 in all cases, the probable error is large; and it will be considered that the coefficients are significant only when they have a value of 0.48 or

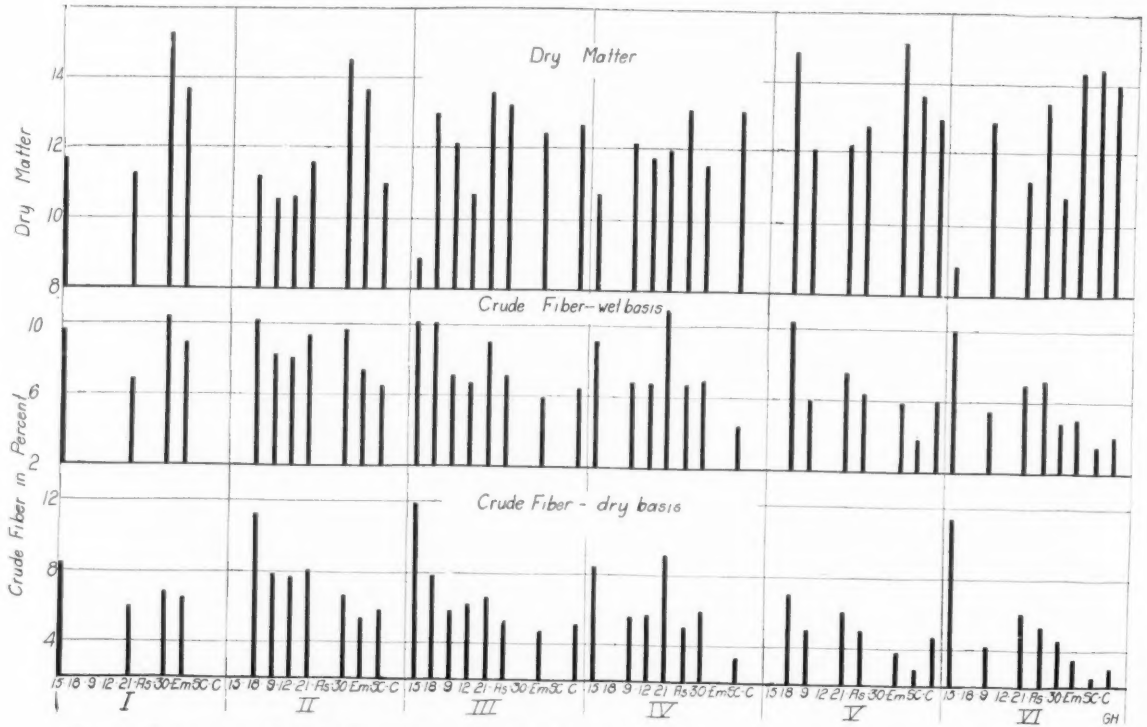

FIG. 3.—Dry matter and crude fiber of 1922 samples of plums, grouped for comparison of varieties at each stage of ripeness; Roman numerals indicate stages of ripeness, numbers and letters indicate names of varieties (latter from left to right in order of increasing susceptibility to brown rot).

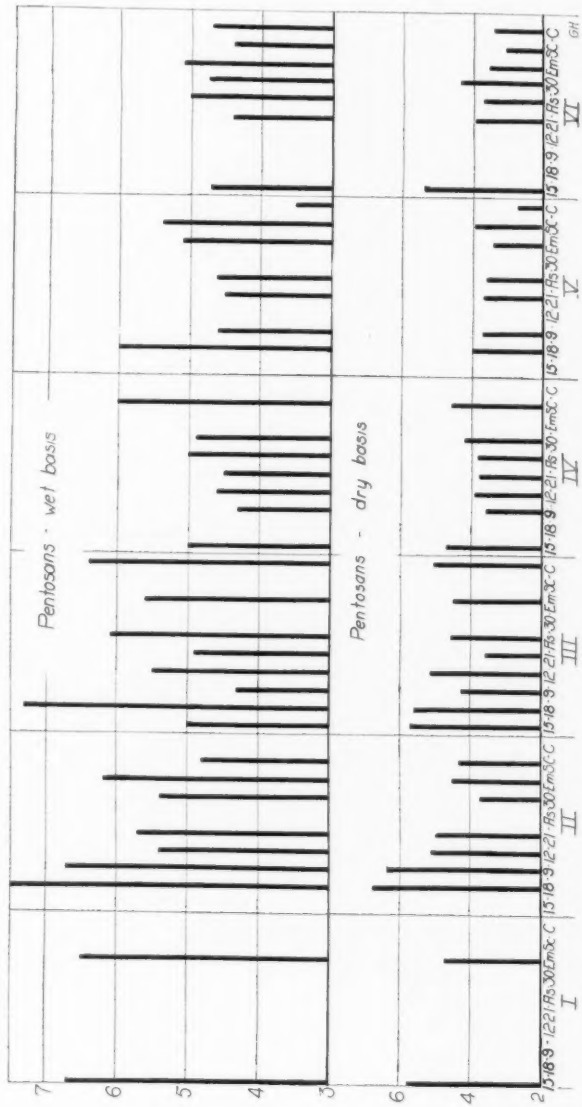

FIG. 4.—Pentosan content of 1922 samples of plums, grouped for comparison of varieties at each stage of ripeness; Roman numerals indicate stages of ripeness, numbers and letters indicate names of varieties (latter from left to right in order of increasing susceptibility to brown rot).

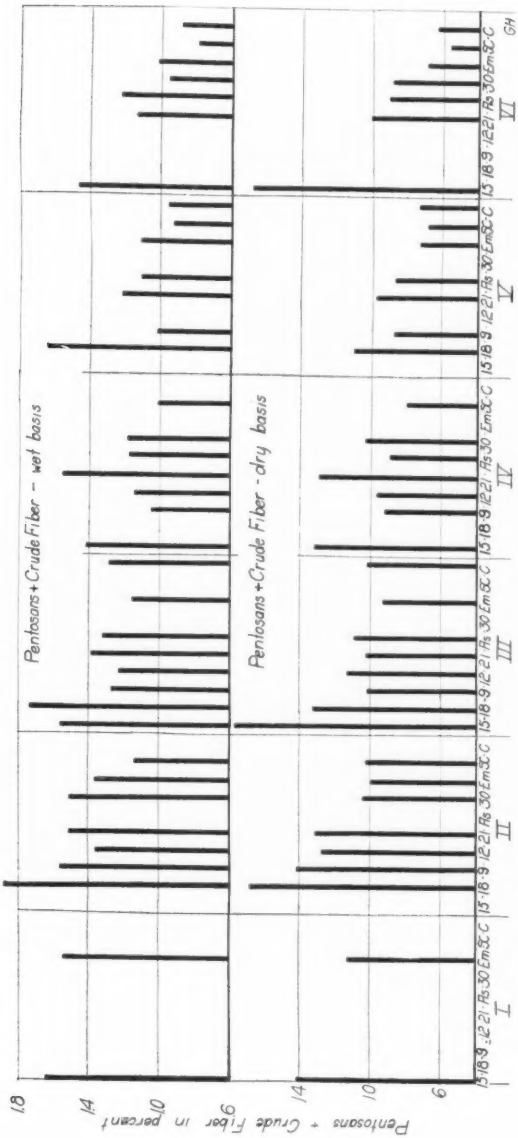

FIG. 5.—Pentosan and crude fiber content added together, and grouped for comparison of varieties at each stage of ripeness; Roman numerals indicate stages of ripeness, numbers and letters indicate names of varieties (latter from left to right in order of increasing susceptibility to brown rot).

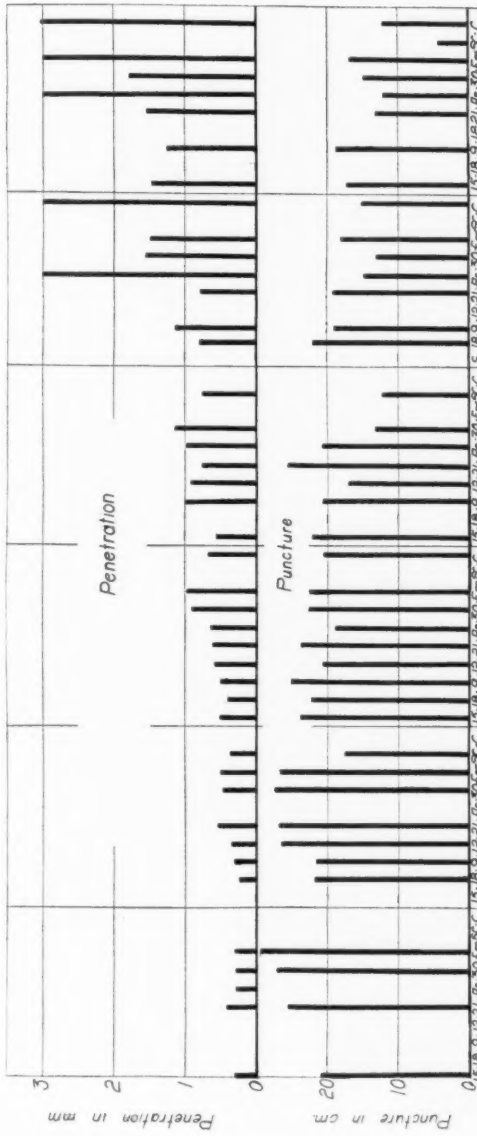

FIG. 6.—Puncture and penetration data of 1922 samples of plums, grouped for comparisons of varieties at each stage of ripeness; Roman numerals indicate stages of ripeness, numbers and letters indicate names of varieties (latter from left to right in order of increasing susceptibility to brown rot).

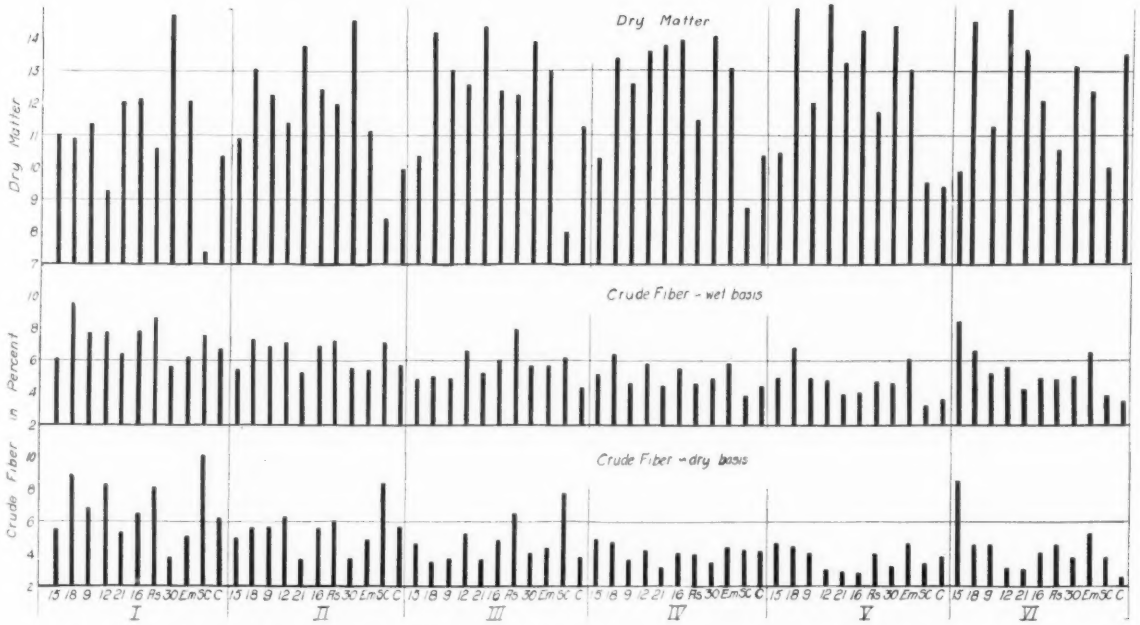

FIG. 7.—Dry matter and crude fiber of 1923 samples of plums, grouped for comparison of varieties at each stage of ripeness; Roman numerals indicate stages of ripeness, numbers and letters indicate names of varieties (latter from left to right in order of increasing susceptibility to brown rot).

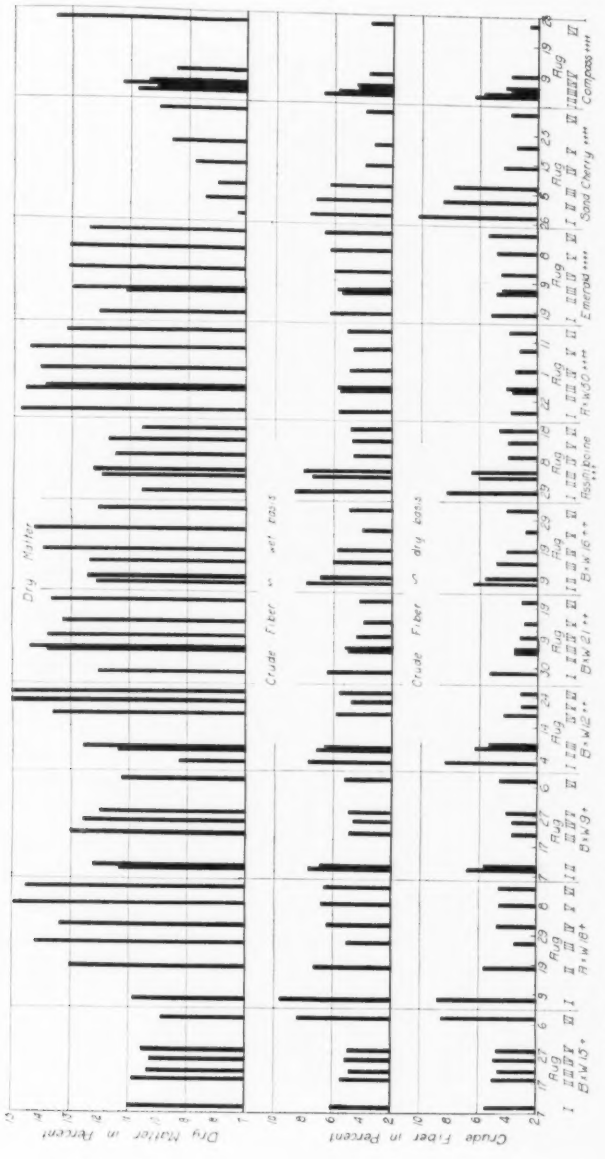

FIG. 8.—Dry matter and crude fiber of 1923 samples of plums, grouped to show progress of ripening in each variety; samples placed according to dates of picking as well as according to stages of ripeness; Roman numerals indicate stages of ripeness, numbers and letters indicate names of varieties (latter from left to right in order of increasing susceptibility to brown rot).

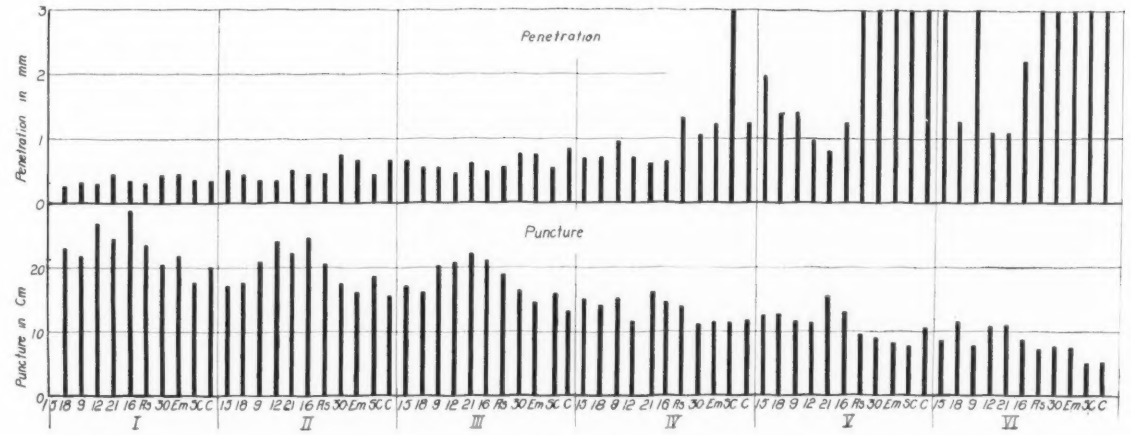
Penetration
Penetration in mm
3
2
1
0
Puncture
Puncture in Cm
20
10
0
I 5 18 9 12 21 16 Rs 30 Em 5C C
II 5 18 9 12 21 16 Rs 30 Em 5C C
III 5 18 9 12 21 16 Rs 30 Em 5C C
IV 5 18 9 12 21 16 Rs 30 Em 5C C
V 5 18 9 12 21 16 Rs 30 Em 5C C
VI 5 18 9 12 21 16 Rs 30 Em 5C C

FIG. 9.—Puncture and penetration data for 1923 samples of plums, grouped for comparison of varieties at each stage of ripeness; Roman numerals indicate stages of ripeness, numbers and letters indicate names of varieties (latter from left to right in order of increasing susceptibility to brown rot).

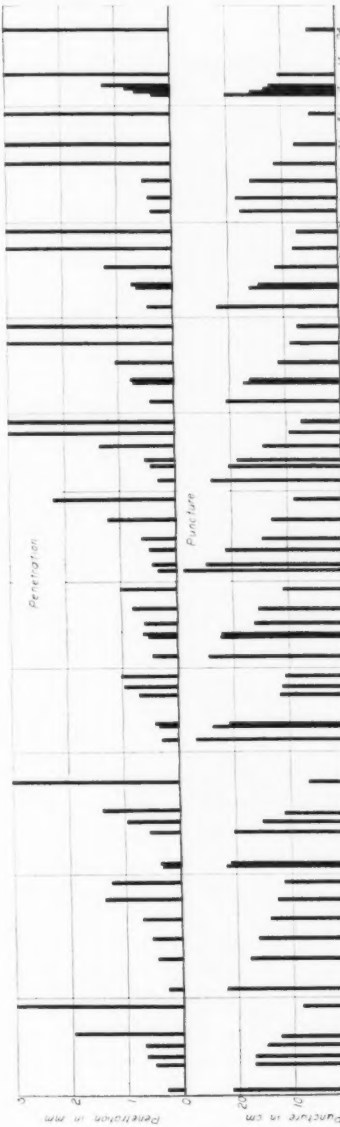

FIG. 10.—Puncture and penetration data for 1923 samples of plums, grouped to show progress of ripening in each variety; samples arranged by dates as well as by stages of ripeness; Roman numerals indicate stages of ripeness, numbers and letters indicate names of varieties (latter from left to right in order of increasing susceptibility to brown rot).

TABLE III

CORRELATIONS BY RANK AMONG VARIOUS FACTORS IN ELEVEN VARIETIES OF PLUMS; DATA OF 1923

STAGE	PUNCTURE AND PENETRATION	PENETRATION AND DRY MATTER	PENETRATION AND CRUDE FIBER (WET BASIS)	PUNCTURE AND CRUDE FIBER (WET BASIS)	DRY MATTER AND CRUDE FIBER (WET BASIS)	PUNCTURE AND DRY MATTER
1	-0.263 ± 0.193	$+0.486 \pm 0.163$	-0.638 ± 0.126	$+0.489 \pm 0.162$	-0.411 ± 0.177	$+0.181 \pm 0.206$
2	-0.664 ± 0.119	$+0.109 \pm 0.209$	-0.630 ± 0.128	$+0.289 \pm 0.195$	-0.057 ± 0.212	$+0.490 \pm 0.179$
3	-0.594 ± 0.155	$+0.037 \pm 0.212$	-0.556 ± 0.147	$+0.289 \pm 0.195$	-0.116 ± 0.210	$+0.346 \pm 0.187$
4	-0.611 ± 0.134	-0.463 ± 0.167	-0.468 ± 0.166	-0.147 ± 0.205	$+0.421 \pm 0.177$	-0.032 ± 0.213
5	-0.762 ± 0.089	-0.477 ± 0.162	-0.075 ± 0.212	$+0.142 \pm 0.209$	$+0.410 \pm 0.177$	$+0.346 \pm 0.187$
6	-0.591 ± 0.141	-0.481 ± 0.162	$+0.064 \pm 0.213$	$+0.518 \pm 0.156$	$+0.027 \pm 0.213$	$+0.345 \pm 0.149$

greater, which is about three times the probable error. It is with these considerations in mind that the values in table III should be scanned. The puncture by penetration coefficients bear negative signs in all stages of ripeness, and they are of significant magnitude in all but the first stage. This means, of course, that a positive relation exists between toughness of skin and firmness of tissue. In table III it will be seen in the green samples (stage I) that softer tissue is correlated with higher dry matter; that the value of this coefficient decreases during the next two stages, and then reverses in sign, so that in the last three stages the firmer tissues are correlated with higher dry matter. The coefficients for penetration and crude fiber are all negative, but they decrease in value regularly from the first to the last stage. This indicates that up to the riper stages a firm flesh is related to a high crude fiber, but that this relation disappears at full ripeness.

A tough skin and high crude fiber occur together in the greenest samples and in the "dead" ripe samples; in the intermediate stages these relations do not hold. The writers interpret this as follows. In the very green and in the very ripe fruits, the skin itself contributes largely to the total crude fiber, due in the first case to the relatively large proportion of skin in the half grown fruit, and in the second case to the disintegration of the fiber of the

flesh during over-ripening. The coefficients for dry matter and crude fiber are of significant magnitude only in stage IV; in the other stages they vary erratically. No explanation for this is offered. In the last column of table III it appears that in the over-ripe samples, soft tissue is related to high dry matter, but that these two factors are not significantly related at any other stage. No explanation of this is offered.

Summary and conclusions

1. The attempt has been made to relate the resistance and susceptibility of plum varieties to brown rot to their chemical and mechanical characteristics. To this end eleven varieties were analyzed at six stages of ripeness during the seasons of 1922 and 1923. Crude fiber, pentosans, and dry matter analyses were made, and the toughness of the skin and the firmness of the flesh were measured.

2. It has been found in general that the resistant varieties have a higher crude fiber content than the susceptible, and that this holds more in the ripe than in the unripe stages of maturity.

3. The pentosan content shows somewhat the same relations to susceptibility as does the crude fiber, but to a less degree. When the two factors are added, in order to get a greater index of the structural elements of the fruit tissue, the relation to susceptibility is more marked than when either is considered alone.

4. Although the toughness of the skin decreases in all varieties as ripeness proceeds, the change is more marked in the susceptible varieties. This is quite in accord with the resistance of plums to brown rot, since varietal differences are not apparent in the greener stages.

5. The firmness of the flesh of plums parallels to a striking degree the toughness of the skin in all stages of maturity. Unquestionably both factors are of importance in conferring resistance on a variety.

6. When the plums become ripe, and especially when over-ripe, these relations tend to disappear; and at these stages practically all varieties become susceptible to brown rot.

7. Coefficients of correlation by rank were calculated for all pairs of factors, and for all stages of maturity, for the 1923 samples. The values obtained verify the generalizations consistently.

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UNIVERSITY OF MINNESOTA

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PHYSIOLOGICAL STUDY OF TWO VARIETIES OF IPOMOEA BATATAS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 338

GEORGE R. JOHNSTONE

(WITH FOUR FIGURES)

Introduction

As an agricultural crop, the sweet potato is second in importance to the Irish potato in the United States. Its production has been increasing in recent years, however, which attaches an increasing importance to the problems of conservation and prevention of losses in storage and in marketing. The average acreage for the years 1910–1914 was 611,000, while in 1920 there were 1,085,000 acres devoted to this crop (**33**). Losses due to disease have been estimated at $58,000,000 for the year 1919. Although improved methods of curing and storing have increased its market value, and have decreased the losses due to decay from 36.23 per cent in 1919 to 21.45 per cent in 1922 (**24**), it is evident that there is great need of fundamental physiological research on cured and uncured sweet potatoes, and on the problems of internal breakdown, discoloration, etc., in different types, in order that more adequate conservation measures may be employed.

The aim of this investigation, therefore, has been to obtain more information regarding the physiology of the sweet potato, particularly with respect to respiration, certain enzymatic activities, and water relations. HASSELBRING and HAWKINS (**10**) studied respiration in the Jersey Big Stem, a dry, firm fleshed variety. Their experiments were carried out at a temperature of 30° C. They found that freshly dug samples increased their rate of respiration for a few days and then the rate decreased. If, however, they were left in the laboratory at 20° C. for 18 days, and then placed in the respiratory apparatus, they reached a maximum rate more quickly. Similar experiments with cured sweet potatoes (that is, those which had been

subjected to a drying process in a well ventilated room at 30° C. for 10 days), after having been stored at 6°–7° C. for 32 days, respired at a much greater rate when placed at the higher temperature for making the determination. This rate gradually decreased to about one half of the maximum on the tenth day, while those which were cured and stored at 12°–15° showed only a slight increase followed by a slight decrease, under the same conditions.

Parallel with these experiments on respiration, analyses were made to determine whether there was any correlation between seasonal changes in sugar content and respiratory activity. Conclusions were negative as to any such general correlations. The respiratory changes effected by splitting the sweet potatoes lengthwise were also determined. Before the roots were split, they respired at the rate of 29.8–42.7 mg. per kilogram hour. After they were split, the rate was 60 mg., which finally decreased to 52.5 mg. on the seventh day. The earlier explanation for the increased respiration of wounded tissues was that wounding acts as a stimulus to increase oxidation. The recent work of MAGNESS (**17**), however, shows that the removal of the epidermal or cortical structures of apples and potatoes is followed by an increase in the oxygen content of the intercellular atmosphere. Since an increase in oxygen pressure is known to hasten respiration of plant tissues, it is probable that the increased respiration occurring in wounded tissues is due largely to facilitation of gaseous exchange in the cut areas. The increased respiration in split sweet potatoes may then be due to an increase in the available oxygen, rather than to other kinds of wound stimulation.

Among other things which have a bearing on the curing and storing of sweet potatoes, is the empirical method suggested by THOMPSON (**31**) for telling when the former process is complete. He referred to the appearance of sprouts as a criterion. MANNS (**19**) has made extensive storage studies. He attributes the loss in weight during storage to the loss in moisture, and recommends a temperature of 55° F., with a relative humidity of 60 per cent for storage. Humidity above 80 per cent is very favorable for storage rots. PRICE (**25**) has found that losses due to harvesting after frost amounted to 67.7 per cent of Porto Rico variety in storage, and 80 per cent of Triumph, as compared with harvesting before frost, when

the losses were only 0.8–1.25 per cent of the first variety and 0.4–5 per cent of the second.

With respect to work on enzymes, GORE (**7**) has determined the diastatic activity for a few varieties of sweet potato, and has worked out a method whereby the contained diastase can be utilized in the preparation of sweet potato sirup. MAGOON and CULPEPPER (**18**) refer to an oxidase as accounting for discoloration of sweet potatoes before cooking, but show no data regarding it. SHERMAN and BALDWIN (**28**) have shown that the optimum hydrogen ion concentration for the activity of three typical amylases varies considerably with reference to the source of the enzyme. The experimental work which follows deals with a number of physiological problems connected with harvesting, storing, and keeping qualities of sweet potatoes, especially with regard to the respiratory and enzymic activities under various conditions, and incidentally to determine whether there is a physiological grouping of varieties comparable with that obtained by STEENBOCK and SELL (**29**), which was based on the fat-soluble vitamine content.

Materials and methods

The sweet potatoes used for the following experiments were obtained from W. A. GARDNER of the Agricultural Experiment Station, Auburn, Alabama, and from J. C. C. PRICE of the Mississippi A. and M. College, Mississippi, to whom my thanks are gratefully accorded. Since most of the material was obtained from the former station, the origin will not be indicated below except when it is from the other source. The approximate 900 miles transit has added to the variable uncontrollable environmental factors which must be taken into consideration.

RESPIRATION.—An apparatus similar to that of MAGNESS (**16**), but adapted for water bath temperature control was used to determine the amount of oxygen taken up and carbon dioxide released during respiration at 25° C. Fig. 1 is a diagram of the apparatus. The apparatus was maintained at 25° C. in a Freas water bath submerged to the point *W*. One hour was allowed for the adjustment of the apparatus to that of the bath, then the separatory funnel was closed. Any significant errors due to vapor pressure, temperature,

etc., were corrected by means of a control apparatus, which was connected with a water manometer for reading very slight changes in volume. The amount of carbon dioxide liberated by the respiring material was determined by titrating an aliquot part of the potassium hydroxide (K), using the double indicator method (**6**). At the end of the experiment the contained gases were again adjusted to

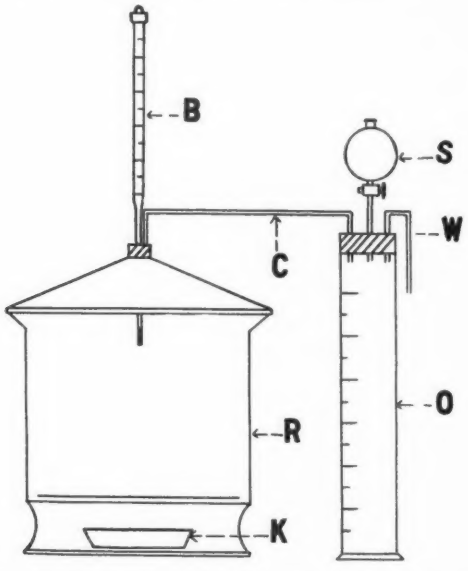

FIG. 1.—Respiratory apparatus adapted for water bath temperature control: R, respiratory chamber; K, 100 cc. potassium hydroxide; B, Beckmann thermometer; C, capillary tube; S, separatory funnel; W, water intake tube; O, oxygen cylinder.

atmospheric pressure at the water level (W), by introducing a little water through the separatory funnel. The volume of water in the oxygen cylinder was taken as equal to the amount of oxygen used by the respiring material. This volume was reduced to standard conditions.

MEASUREMENT OF INTERCELLULAR GASES.—The apparatus designed by MAGNESS (**17**) was used for taking samples of the intercellular gases, which were transferred for analyses to the Bonnier-Mangin apparatus as described by AUBERT (**2**).

EFFECT OF INJURY ON RESPIRATION.—Two sets of material from the same variety, Porto Rico, were tested for normal respiration, and then a plug was cut out of each potato by means of a cork borer 16 mm. in diameter. The plugs of one set were replaced and sealed, while they were left out of the other set, but included in the respiratory chamber. An equal normal area of the latter was sealed to correspond to that of the former, and then the respiratory activity of each set was determined in the usual manner.

MOISTURE DETERMINATIONS.—The stem half was used in each case for moisture determination. It was ground on a potato grater to a fine pulp, and 4–6 gm. samples of it were placed on tared watch glasses and weighed. The material was then covered with 95 per cent alcohol, and dried to constant weight at 60° C. in a vacuum oven at reduced pressure.

CURING TEMPERATURE AND REGENERATION.—Sweet potatoes kept at 30° C. for 10 days in the curing house frequently develop shoots 2–4 cm. long or longer. The question has occurred as to whether the development of these shoots was initiated by the higher temperature, or by a less likely cause, namely, the loss of water which occurs during the process. In order to obtain some information bearing on this question, two similar lots were selected, and placed in desiccators at 27–30° C. for a period of 10 days. The bottom of one desiccator was covered with water, while a dish of $CaCl_2$ was placed in the other. Air was drawn through both desiccators by means of a suction pump. The air drawn through the former was first bubbled through concentrated sulphuric acid and then through water, so that a nearly saturated atmosphere was maintained practically free from ammonia and other obnoxious gases. In the other desiccator, a dry atmosphere was maintained by drawing air into it through a calcium chloride tube and then through concentrated sulphuric acid.

HYDROGEN-ION CONCENTRATION.—By means of the hydrogen electrode, the hydrogen-ion concentration of the expressed juices of each variety was determined. After equilibrium in the solutions being tested was established, readings in millivolts on the type *K* potentiometer were made, and later converted into P_H values, correcting for temperature according to the method described by MICHAELIS (**20**).

CATALASE.—The apparatus used and the method employed for the determination of catalase activity were essentially those of APPLEMAN (1). Because of insufficient material, it was impossible to take the juice from portions of several sweet potatoes to test as an average, so one was selected as representative of the lot. The first inch of the stem end was discarded; then by means of a 10 mm. cork borer, a central cylinder from the next inch was removed and placed into a glass stoppered weighing bottle. Each test consisted of four or five determinations, by weighing out different quantities so as to include the mass of material which would give the optimum or very nearly the optimum activity with 5 cc. of standardized hydrogen peroxide, neutralized with calcium carbonate. Each weighed sample of material was triturated in a mortar with a small amount of clean sand, and an equal amount of calcium carbonate. All determinations were made at 25° C., and the volume of oxygen liberated was reduced to standard conditions.

AMYLASE.—WOHLGEMUTH'S (9) method was used to demonstrate the presence of amylase. One hundred gm. of the pulp were extracted for one hour at 25° C. with 200 cc. of distilled water, and 1 cc. of toluene was added as a preservative. The extract was filtered through a creased filter paper, and its amylolytic activity was determined by use of a series of 10 test-tubes, each containing 5 cc. of a 1 per cent solution of Merck's soluble starch, maintained at 0° C. in ice water until the extract to be tested was added. The amount of diastase extract was varied, so that the series ranged from 0.2 cc. to 2.0 cc. The preparations were then incubated at 38° C. for 30 minutes, and again returned to the ice water to check hydrolysis. Of those tubes which showed no blue color with N/10 iodine solution, the one that contained the most extract was selected as the standard, and the activity was calculated for 1 cc. of the extract for comparative results expressed as $D38° 30'$. D equals the number of cubic centimeters of 1 per cent starch solution hydrolyzed at 38° C. during a period of 30 minutes (table IX).

LACCASE AND PEROXIDASE.—The following reagents were used to demonstrate the presence of laccase: 0.5 per cent alcoholic solution of gum guaiacum (13), and a 1 per cent aqueous solution of tetramethylparaphenylendiamine hydrochloride (32). These reagents

were used separately by applying them directly to the tissues, and noting the time required for definite color changes to take place. The organic peroxide which was demonstrated to be present by means of starch, KI solution, and acetic acid, was destroyed by heating the juice or tissue to 50° C. for a few minutes. Tests for peroxidase were made by treating the juice or tissue with the same solution of guaiacum previously described in the presence of hydrogen peroxide. Benzidine with hydrogen peroxide seemed to be less satisfactory. The oxidase system, which will be mentioned later, refers to the functioning of the so-called enzymes, laccase and peroxidase, which account for the discoloration of the tissue on exposure to air.

Experimental data

RESPIRATION AT DIFFERENT DATES OF HARVESTING.—Fortunately no rains occurred in the field where the sweet potatoes were growing until October 16, so that a considerable number of data

TABLE I

RESPIRATION OF UNCURED SWEET POTATOES AT DIFFERENT DATES OF HARVESTING

DATE OF HARVEST	DAYS IN TRANSIT	RATE OF RESPIRATION PER KGMHR							
		Porto Rico				Triumph			
		CO_2 (mg.)	CO_2 (cc.)	O_2 (cc.)	CO_2 / O_2	CO_2 (mg.)	CO_2 (cc.)	O_2 (cc.)	CO_2 / O_2
September 1.....	6	42.63	21.71	24.61	0.882	38.80	19.76	20.71	0.954
September 1.....	7	42.99	21.89	22.28	0.982	38.13	19.42	17.55	1.10
September 14....	9	52.92	26.95	20.59	1.300	37.40	19.04	.....	.....
September 14....	10	57.06	29.06	27.72	1.040	39.50	20.11	15.13	1.32
September 27....	8	56.62	28.83	27.26	1.050	37.33	19.01	14.25	1.33
September 27....	9	73.02	37.19	35.63	1.043	.....	.....	.....	.....
October 25.....	5	50.17	25.55	22.51	1.145	37.94	19.32	15.54	1.24
October 25.....	9	85.17	43.38	42.60	1.018	43.17	21.98	21.63	1.01

were obtained during favorable weather conditions. Table I shows the rates of respiration for the two varieties at different times of harvesting.

Respiration in the first three sets harvested was determined on two successive days, as indicated in the data of table I. On the

second day in every case there was an appreciable increase. The increase in the rate was more pronounced when the second determination was made after a longer interval, as shown by the data for those harvested October 25. Fig. 2 shows the progress of respiration in storage for the two varieties of uncured sweet potatoes.

Cured sweet potatoes do not reach as high a maximum of respiratory activity as uncured samples under approximately the same conditions of storage, as shown by the curves in fig. 3 compared with those in fig. 2.

The slight increase in respiration shown by the curves on the fourth to seventh days is undoubtedly due to transferring the sweet potatoes to the higher temperature for respiration determination,

TABLE II

RESPIRATION AND TRAUMA AT 25° C., PORTO RICO VARIETY

TREATMENT	WEIGHT OF SAMPLES (GM.)		AREA OF INJURED SURFACE IN MM.²	CO_2 RELEASED PER KGMHR (MG.)		PERCENTAGE INCREASE
	First	Final		Before injury	After injury	
Plugs removed	632	623	7385.3	64.27	126.81	97.30
Plugs replaced and sealed	632	628	7636.4	60.06	70.36	17.15

but cured sweet potatoes do not respond as readily to such a change of condition as the uncured.

RESPIRATION AND TRAUMA.—THOMPSON (31) reports that the minimum shrinkage under commercial handling was 7.40 per cent, and maximum 20.40 per cent, with an average of 10 per cent for several lots. The average amount of decay was 0.45 per cent under careful handling and 3 per cent under commercial handling. The data of table II have a bearing on the cause of shrinkage due to commercial handling, but would not account for all of it. One may conclude from this that the part of shrinkage due to respiration, although it may be small, is very much greater when the cortical layer is broken, and that such increase is largely due to facilitating the exchange of gases rather than to direct wound stimulation.

ANALYSIS OF INTERCELLULAR GASES.—Relatively large samples of gas could easily be obtained from cylindrical plugs cut out by

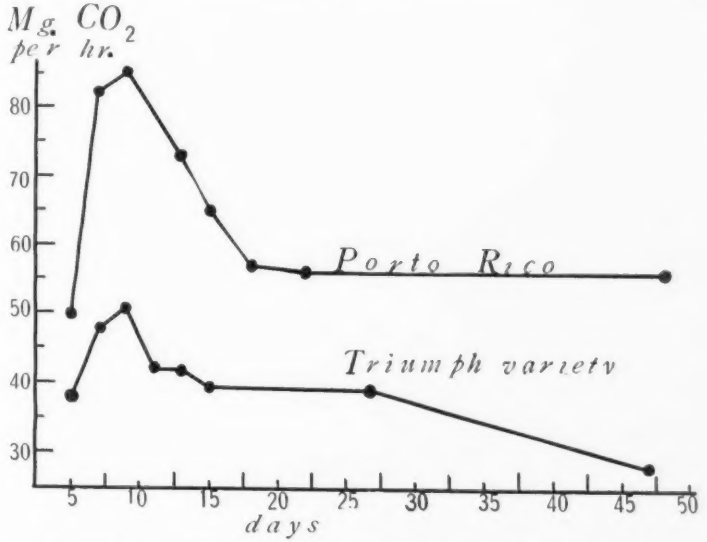

FIG. 2.—Progress of respiratory activity determined at 25° C. at various intervals from date of harvesting for two varieties of sweet potatoes stored in basement at 15°–20° C.

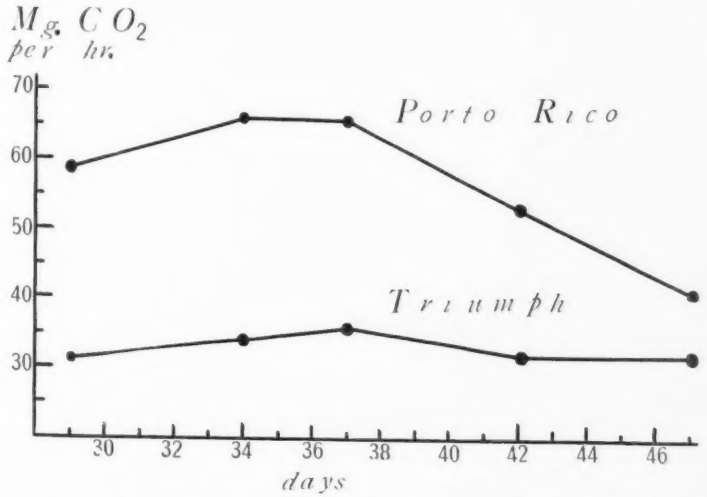

FIG. 3.—Progress of respiration determined at 25° C. for two varieties of cured sweet potatoes in basement storage at 15°–20° C.

means of a 22 mm. cork borer. Gas was drawn out of these plugs by placing them in an apparatus designed by MAGNESS (**17**). Although a great many determinations were made, only a few typical analyses are given in table III. The larger amount of carbon dioxide in the tissues of Porto Rico variety may be explained as due to the greater rate of respiration which occurs in that variety. Any difference in the porosity of the tissues of the two varieties, or any factor which would facilitate the exchange of gases, would influence the CO_2/O_2 ratio.

RESPIRATORY COEFFICIENT.—Q_{10}, or the coefficient for each 10° rise in temperature, has been worked out for respiration of a number

TABLE III

ANALYSIS OF INTERCELLULAR GASES

DATE OF HARVEST	DATE OF DETERMINATION	PERCENTAGE	
		CO_2	O_2
	Porto Rico		
October 25.....	November 9	7.086 7.732	15.74 14.95
	Triumph		
October 25.....	November 7	6.770 6.780	15.62 16.13

of plants. In raising the temperature of the apparatus and the material each 10° a source of error was found, depending on whether the determination was begun immediately, or not until the material had been raised to the desired temperature. If the latter method was used, which was more accurate, the error could not entirely be eliminated, because the material had to be taken out of the respiratory apparatus in order to introduce fresh alkali. This procedure permitted the temperature of the material and the apparatus to fall so as to introduce an error. Both methods were used, and the latter, as expected, gave a steeper curve for the rate of respiration. Both varieties used in these experiments were obtained from the Mississippi Experiment Station. They had been cured and apparently

were in good condition, although the experiments were begun March 26.

RESPIRATION AT HIGHER TEMPERATURE.—Porto Rico variety was used for these determinations. They were cured sweet potatoes from the Mississippi A. and M. College, stored since March 4 in the basement at 15°–20° C. In each determination the sweet potatoes were placed in the oven, outside of the respiratory chamber, until their temperature reached that of the oven as indicated by a thermometer inserted into a control sweet potato. When the temperature of its interior became equal to that of the oven, the other sweet potatoes were placed in the respiratory chamber. Thus the period of "preliminary" heating was different for each of the three higher temperatures, being one and one-third hours for the experiment conducted at 44° C., three hours for that at 50°, and five hours for the 55° series. The curves in fig. 4 indicate the nature of respiration at these temperatures.

TABLE IV

TEMPERATURE COEFFICIENT OF RESPIRATION, Q_{10}

TEMPERATURE °C.	CO_2 PER KGMHR (MG.)	Q_{10}	MG. CO_2 PER KGMHR	Q_{10}
	Porto Rico		Triumph	
15	37.35	.....	27.64	.....
25	79.22	2.121	63.31	2.29
35	121.05	1.528	110.73	1.748

The potassium hydroxide which was used to collect the carbon dioxide was changed every two hours for ten hours, titrating it each time to determine the carbon dioxide content.

BLACKMAN (5) has already observed this temperature effect. When a process is determined as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the slowest factor. He refers to the optimum by some investigators as the highest temperature which can be permanently sustained without depression of function, but more usually a real optimum is held to be characterized by this, that the retardation produced by exposure to superoptimal temperature must not be of the nature of

permanent injury, and that therefore on cooling again to the optimum temperature there must be a return of the function to its highest value. The curve for respiration at 44° C. (fig. 4) shows a slight falling off in the rate.

MOISTURE DETERMINATIONS.—These measurements were made in the usual manner as soon as the material arrived at the laboratory. The first six lots of sweet potatoes had not been cured, while the

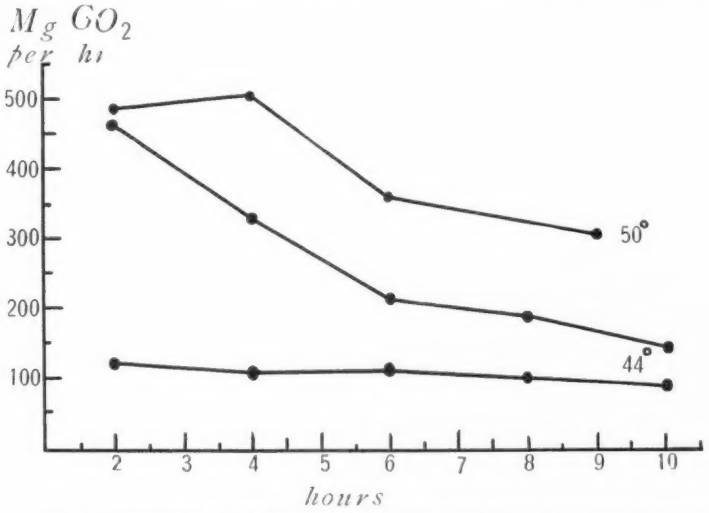

FIG. 4.—Respiration at higher temperatures for cured Porto Rico sweet potatoes; March, 1924.

seventh or last lot was cured. The dates of harvest and dates of moisture determinations are indicated in table V.

It was impossible to take the moisture determinations immediately after curing, because of the delay in transit from Auburn, Alabama. This delay, to a certain extent, would account for the increase in moisture content of Porto Rico variety after curing.

In order to obtain more accurate data regarding the effect of curing on the moisture content, samples of Triumph variety were placed in two desiccators. A moist atmosphere was maintained in one by means of a layer of water, while calcium chloride was placed in the other desiccator to maintain a dry atmosphere. By means of a

suction pump, a continual stream of air was drawn through each desiccator. The air was first drawn through a bottle of sulphuric acid and then through water, to maintain a moist atmosphere in one

TABLE V

MOISTURE DETERMINATIONS AT DIFFERENT DATES OF HARVESTING

DATE OF HARVEST	DATE OF DETERMINATION	PERCENTAGE MOISTURE	
		Porto Rico	Triumph
August 2	August 9	76.11	73.07
		76.29	73.52
August 21	August 25	72.49	72.50
		72.37	72.39
September 1	September 6	72.50	68.15
		72.22	68.07
September 14	September 21	68.92	65.15
		68.54	65.95
September 27	October 4	69.09	67.48
		68.82	67.04
October 25	October 30	65.80	63.62
		65.66	63.75
October 25	November 23	68.24	60.92
Cured		68.01	60.95

apparatus, but drawn through a calcium chloride tube and then through sulphuric acid, to supply a dry atmosphere in the other. Table VI shows data for this experiment. These data show that

TABLE VI

EFFECT OF CURING ON MOISTURE CONTENT OF TRIUMPH VARIETY

PERCENTAGE MOISTURE IN FRESH MATERIAL	PERCENTAGE MOISTURE AFTER 10 DAYS AT 30° C.			
	Dry atmosphere	Loss	Moist atmosphere	Gain
68.15	67.20	.....	71.76	.....
68.07	67.30	.....	.....	.....
Average 68.11	67.25	0.86	71.76	3.65

there is not much gain or loss in the moisture content as influenced by that of the atmosphere.

CURING TEMPERATURE AND REGENERATION.—In order to determine whether regeneration during the curing process was due to the decrease in moisture content, or to the higher temperature main-

tained during the process, sweet potatoes were placed in moist and dry atmospheres at the usual curing temperature. These atmospheres were continually being changed by continuous streams of air maintained by a suction pump, as already described. Results showed that roots and shoots both developed in the moist atmosphere, while shoots only, or no growth at all, occurred in the dry atmosphere. It is evident, therefore, that the higher temperature is the main external factor in promoting growth, and that lack of moisture retards growth. The appearance of shoots is not necessarily a good index for complete curing.

HYDROGEN-ION CONCENTRATION OF EXPRESSED JUICES.—Determinations, by means of the hydrogen electrode, were made at

TABLE VII

HYDROGEN-ION CONCENTRATION OF EXPRESSED JUICES

DATE OF HARVEST	DATE OF DETERMINATION	PORTO RICO			TRIUMPH		
		Millivolts P_D	Temperature	P_H	Millivolts	Temperature	P_H
August 21	August 25	619.8	24.5	6.33	620.6	25	6.34
September 1	September 10	612.4	22.0	6.23	608.8	22	6.17
September 14	September 21	612.6	21.0	6.26	609.0	22	6.17

various intervals. Table VII shows data for these determinations. The data show that there is not much difference in the hydrogen-ion concentration of the expressed juices of the two varieties. This is most likely due to the buffer action of the various substances present. Some proteins were included, since the juice was separated from the pulp by pressing it through a cloth.

CATALASE ACTIVITY.—A number of determinations of catalase activity have been made. In every case when the material had been under the same conditions of treatment, the Porto Rico variety gave higher catalase activity. In preliminary experiments with material which had deteriorated in storage, curves for catalase activity obtained were very irregular. Table VIII shows data for normal tissue. These data show that both moisture and catalase activity are higher in Porto Rico variety than in Triumph.

AMYLASE ACTIVITY.—WOHLGEMUTH'S method was used and found to be very convenient for comparative purposes. A test was also made to determine the influence of varying the hydrogen-ion concentration on amylolytic activity under the conditions of the

TABLE VIII

CATALASE ACTIVITY OF UNCURED SWEET POTATOES HARVESTED DURING SEPTEMBER AND OCTOBER

DAYS SINCE HARVEST	PORTO RICO				TRIUMPH			
	Weight of tissue (gm.)	O_2 liberated (cc.)	Rate per gm.	Percentage HOH	Weight of tissue (gm.)	O_2 liberated (cc.)	Rate per gm.	Percentage HOH in tissue
13	0.1283	13.96	107.5	72.3	0.2807	28.01	99.79	68.11
8	0.3181	46.16	176.5	68.7	0.3891	18.27	46.96	65.55
9	0.3230	37.90	117.3	68.9	0.3990	40.37	117.17	67.27
10	0.2298	38.87	196.1	65.7	0.3145	26.94	85.66	63.68
Average	0.2498	.....	149.3	.....	0.3458	.....	87.39	.....

experiment. Three indicators, Congo red, litmus, and phenolphthalein were used to prepare media with three different P_H values, approximately 5, 7, and 9. Amylase activity was found to be the same in the last two, but less active in the first, with a P_H value of approximately 5. Several additional determinations were made with material in varying conditions of storage, curing, etc. Results showed values as high as 12 for amylolytic activity in some cases.

TABLE IX

AMYLASE ACTIVITY OF SWEET POTATO EXTRACT, JANUARY 5

PREVIOUS TREATMENT	PORTO RICO		TRIUMPH	
	Amylase extract (cc.)	$D^{38°}_{30'}$	Amylase extract (cc.)	$D^{38°}_{30'}$
Harvested October 25, cured	0.6	8.33	1	5
Harvested September 14, uncured	0.6	8.33	1	5

LACCASE.—This oxidase enzyme was shown to be present in both varieties by means of treatment with tetramethylparaphenylendiamine hydrochloride, and qualitative-quantitative tests were made with guaiacum on material at different times of harvest, after it had

been in storage 3.5–5 months. Table X shows data for these determinations. While the guaiacum test is only qualitative-quantitative, the data indicate that laccase had been inactivated, due to conditions initiated by the heavy frost which occurred January 1, or the organic peroxide which functions with peroxidase had been destroyed.

ABSENCE OF TYROSINASE.—By redissolving the alcoholic precipitate from the aqueous extract of each variety, and by testing it with a suspension of tyrosin, no apparent discoloration occurred even after twelve hours, while in the control containing an aqueous solution of tyrosin a slight pink color developed. As a check on the

TABLE X

LACCASE AND PEROXIDASE ACTIVITY DETERMINED BY BLUING OF GUAIACUM, APRIL 14, 1922; FIRST KILLING FROST, JANUARY 1

DATE OF HARVEST	PREVIOUS TREATMENT	TIME IN SECONDS FOR BLUING OF GUAIACUM		DATE OF HARVEST	PREVIOUS TREATMENT
		Porto Rico	Triumph		
October 12.....	None	5	3	October 12	None
November 30....	None	5	6	November 2	None
December 7.....	None	4	4	December 7	None
December 7.....	Tops removed October 5	3	4	December 7	Topped October 5
January 11.....	Topped November 9	10	.....	.....	.....
January 11.....	No treatment	10	.....	.....	.....

method, an alcoholic precipitate from the juice of the Irish potato was prepared, redissolved, and tested in exactly the same way with a tyrosin solution. In a short time a pink color developed which was followed with black. Furthermore, a preparation from the Irish potato known to contain tyrosinase (4) was added to the juice and pulp of the two varieties. No apparent discoloration occurred, indicating that tyrosin does not occur in the sweet potato varieties tested.

PEROXIDASE.—Qualitative tests were made for peroxidase by treating the tissue with guaiacum and hydrogen peroxide. Oxidation of the guaiacum to guaiacum blue under these conditions was more rapid in every case, indicating the presence of peroxidase.

Further tests were made to distinguish laccase from peroxidase.

BACH'S (3) method for distinguishing laccase from tyrosinase suggested a way for distinguishing laccase from peroxidase. Laccase is thermostable at 70° C., while the organic peroxide which is necessary for the action of peroxidase without the addition of hydrogen peroxide is thermolabile at 60° C., or at 55° if the sweet potatoes are placed in an oven for several hours at the latter temperature. Table XI shows data for several determinations.

The data in table XI suggest an oxidase system which would account for discoloration. This system consists of laccase, which activates the oxygen of the air directly or by forming a temporary

TABLE XI

TESTS FOR LACCASE, PEROXIDASE, ORGANIC PEROXIDE, AND TANNIN IN PORTIONS OF PORTO RICO SWEET POTATO; −=NEGATIVE TEST; *=POSITIVE; **=VERY STRONGLY POSITIVE

PORTION USED	TEST FOR LACCASE		TEST FOR PEROXIDASE	ORGANIC PEROXIDE TEST, KI, STARCH, CH_3COOH	TANNIN TEST WITH DILUTE $FeCl_3$
	Tetramethyl-p-phenylen-diamin HCl	Guaiacum	Guaiacum plus H_2O_2		
Fresh juice, healthy	***	*	**	*	**
Same, boiled	−	−	−	−	**
Fresh juice, wilted	**	*	**	**	**
Same, boiled	−	−	−	−	**
Control HOH	−	−	−	−	−
Slices, healthy	*	*	**	*	*
Same, wilted	**	**	**	*	***
Heated at 55° C. six hours	*	*	**	−	*

peroxide independent of the organic peroxide which worked in conjunction with peroxidase. The chromogen involved is probably a tannoid substance.

PHYSIOLOGICAL GROUPING.—The data in tables I, III, IV, V, VIII, XI, and figs. 2 and 3 suggest that there is a physiological grouping. The Porto Rico variety has higher respiratory activity, its moisture content is higher, and those enzymes which were studied quantitatively were more active in every case. This suggested grouping corresponds to the grouping of varieties found by STEENBOCK and SELL (29), which was based on fat-soluble vitamines referred to under Methods. Porto Rico variety represents the group that is high in fat-soluble vitamines.

Discussion

The changes which take place during the curing of the sweet potato are largely physiological, marked mostly by an increase of respiration for a few days after harvesting until a maximum is reached and then a gradual falling off to a nearly constant rate. These changes seem to take place regardless of the temperature, within reasonable limits, but the process is augmented by a temperature of 30° C., which is commonly used. An appreciable loss in weight occurs during the curing process, due to respiration accompanied by conditions favorable for the removal of carbon dioxide and excess water. The moisture content remains about the same, usually with a slight loss. Data in table V show a possible loss of 3.2 per cent from Porto Rico and 2.33 per cent from Triumph variety. In the interpretation of such data, it is necessary to take into consideration the fact that the sweet potatoes were subjected to uncontrollable environmental conditions in transit of approximately 900 miles by express. More exact data in table VI indicate a much smaller loss of moisture during the curing process than ordinarily believed. HASSELBRING (**11**) found for Big Stem a loss of 0.51 per cent, and for Southern Queen 3.28 per cent of moisture during the curing process followed by a few days in storage. He found that sugars increase and starch decreases during this same period.

Respiration in the sweet potato is relatively high as compared with that of the Irish potato, especially when the latter is in a dormant condition. Curing finally decreases the rate of respiration in the former. This might account for the increase in total sugars as found by MAGOON and CULPEPPER (**18**). Just as respiration decreasing at low temperatures is accompanied by accumulation of sugars (**21**), so the accumulation of sugars during the curing process may be related to the final decrease in respiration.

STICH (**30**) showed that by cutting the Irish potato in four parts, a considerable increase in the rate of respiration followed. MAGNESS (**17**) and SHERMAN (**27**) raised the question as to what extent respiration under those conditions is due to facilitating the exchange of gases, and to what extent it is due to direct stimulation. Data in table II show that the increase is largely due to the former. This also has a bearing on the explanation of shrinkage under commercial handling.

The discoloration mechanism, according to the data presented, seems to be a two-phase oxidase system. One phase consists of peroxidase and an organic peroxide comparable with that described by OVERHOLSER and CRUESS (**22**) in their study of the browning of apple tissue, and earlier described by KASTLE and LOEVENHART (**13**). The other phase seems to be another enzyme, laccase, which activates oxygen without the presence of the same organic peroxide of the first phase. RACIBORSKI (**26**), in his studies of sugar cane, found that after heating the cane to 60° C. no action followed with guaiacum, unless hydrogen peroxide was added. This would suggest a one-phase peroxidase organic peroxide system, in contrast with the two-phase system found in the sweet potato.

Very little evidence has been presented regarding the chromogen which is oxidized in the system. $FeCl_3$ indicated the presence of a tannoid substance. KOHMAN (**14**) attributes the discoloration of canned sweet potatoes to the action of iron on tannin compounds forming an insoluble substance.

The relatively large intercellular spaces may undoubtedly facilitate exchange of gases. The more rapidly respiring Porto Rico variety was found to have a higher percentage of carbon dioxide in the intercellular spaces. MAGNESS (**17**) found that by the removal of a part of the epidermis of the apple, there followed a decrease in the carbon dioxide of the intercellular spaces, most likely due to the facilitation of gaseous exchange.

In consideration of the influence of higher temperatures on the rate of respiration, BLACKMAN'S (**5**) temperature effect has been referred to, that when a process is determined as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the slowest factor. Q_{10}, or the temperature coefficient for respiration in sweet potatoes, ran a little low for ARRHENIUS' temperature law for chemical reactions, where the coefficient is between 2 and 3. The coefficient for respiration in sweet potatoes is more nearly that of a heterogeneous system where two processes occur, the one retarding the other. GORE (**8**), however, found respiratory coefficient in fruits to be 2.38.

With respect to regeneration in the sweet potato, it is commonly known that adventitious buds arise from the stem end of the roots which are used for propagating. MCCALLUM (**15**) defined regenera-

tion as the replacement of an organ or structure that has been removed. The shoots referred to on the sweet potato are potentially new individual plants. That they are formed during curing seems to be significant in showing that the dormant period in this case depends on lower temperature.

It has been commonly recognized that Porto Rico variety is more popular in northern markets because of its edible qualities. It is soft fleshed, and seems to be sweeter than Triumph. Physiological grouping of varieties is suggested by the greater respiratory and enzymatic activity of the former variety as compared with the latter. This distinction is comparable with STEENBOCK and SELL'S grouping, based on fat-soluble vitamine content. Porto Rico represents the orange-yellow fleshed varieties, while Triumph represents the white fleshed varieties. When they did their work, it was thought that possibly the yellow pigment in the former variety might act as a growth promoter. This was investigated by PALMER (**23**), and found to have no significance.

Summary

1. Freshly dug sweet potatoes, varieties Porto Rico and Triumph, increase in their rate of respiration apparently from the date of harvest until a maximum is reached, and then the rate gradually falls to a nearly constant level.

2. Cured sweet potatoes do not reach so high a maximum rate of respiration under the same conditions of storage and experimental procedure.

3. Curing decreases the rate of respiration.

4. Increase of respiration as a result of injury when the cortical layer is broken is largely due to facilitating the exchange of gases, rather than to direct wound stimulation.

5. Curing under carefully controlled conditions does not reduce the moisture content to any great extent.

6. Porto Rico variety has a larger percentage of carbon dioxide in the intercellular spaces than Triumph, under the same conditions of storage and treatment.

7. Respiration in both varieties responds to each 10° rise in temperature in much the same way between 15° and 35° C., having

nearly the same respiratory coefficients. The former variety respires at the greater rate.

8. Regeneration frequently occurs during the curing process, which indicates that dormancy depends on the existence of lower temperature, approximately 25° C. and lower.

9. The hydrogen-ion concentrations of the expressed juices are about the same in each variety, being slightly acid.

10. Moisture and catalase activity are higher in Porto Rico variety than in Triumph.

11. Both laccase and peroxidase are present in Porto Rico variety. These enzymes seem to be important in connection with discoloration of the tissues on exposure to the air.

12. Laccase is thermostable at 60°–70° C., while the organic peroxide of the peroxidase-oxidase system is thermolabile at 60°–65° C.

13. The oxidase system seems to be injured by changes initiated by chilling.

14. Amylase activity varies considerably with storage conditions and treatment. Optimum activity occurs in a medium with a P_H value of 7–9, with a marked falling off at P_H 5. Amylolytic activity of Porto Rico is greater than that of Triumph.

15. Tests for tyrosinase were negative in each variety.

16. A physiological distinction of the two varieties is evident. Porto Rico has greater respiratory activity, greater enzymatic activity, and a higher moisture content.

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TRANSECT METHOD OF STUDYING WOODLAND VEGETATION ALONG STREAMS

J. E. Weaver, Herbert C. Hanson, and John M. Aikman

(with eleven figures)

In pursuance of an investigation of competition among certain shrubs (*Rhus glabra*,[1] *Corylus americana*, *Symphoricarpos* spp.), and between these shrubs and *Quercus macrocarpa*, it became imperative, for a proper understanding of their behavior, to ascertain just how near the edge of their range they were growing. The station, which is located at Weeping Water, Nebraska, is on the Weeping Water River, a branch of the Missouri, 15 miles west of its mouth. This stream arises 15 miles farther west, and in general its course parallels that of the Platte River about 15 miles north. As is generally the case throughout eastern Nebraska, chaparral and woodland are confined to the vicinity of the stream courses. Rather than following the meandering stream throughout its length, it was decided to make transects at six or seven places, thus saving much time during a busy field season. The results were so interesting, and the method so satisfactory in vividly portraying distribution with change of habitat, that it was repeated on the Little Nemaha River, a neighboring stream of similar size and general direction of flow. Unlike the Weeping Water, which cuts a deep canyon, this stream has a broad flat floodplain.

The initial transect was made at the headwaters, about 2 miles northeast of Eagle. Here the unbroken (but pastured) prairie sloped to form a broad valley, in only the lower part of which an intermittent stream, dry nearly all summer, had begun to cut a channel. *Salix nigra* occurred as isolated individuals or in intermittent clumps (fig. 1). Aside from a few *S. amygdaloides* and *Populus deltoides*, no other trees were represented, and there were no shrubs. Similar vegetation prevailed for two miles, although the channel became well defined, often with steep banks 4 or 5 feet high.

[1] Nomenclature is according to Britton's *Manual of the flora of the northern states and Canada*. 2d ed.

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FIGS. 1, 2.—Fig. 1, willows (*Salix nigra*) at headwaters of Weeping Water River; fig. 2, development of stream in transect 3; elms and cottonwoods characteristic trees.

The second transect, which, like the first, included nearly a mile of the stream course, showed marked changes. The spring-fed stream ceased to be intermittent. It had cut banks 10–20 feet wide, and in places 8–10 feet deep, through the broad, prairie covered valley. In a few meanders, broad, somewhat wind protected sloping banks had been formed above the general channel. These were favorable places for a scattered growth of shrubs, chief among which were *Symphoricarpos symphoricarpos*, *S. occidentalis*, *Sambucus canadensis*, *Prunus americana*, and *Amorpha fruticosa*, the last growing down to the water's edge. *Ribes gracile*, *Rhus glabra*, *Celastrus scandens*, and *Vitis vulpina* were also found, but they were rare. *Salix nigra* was dominant, with considerable *S. amygdaloides*, the trees being much larger than before (some 2 feet in diameter) and much more abundant. A single small specimen of *Fraxinus lanceolata* and two of *Prunus virginiana* were the only other woody plants.

A third transect 2 miles beyond and just northwest of Elmwood gave a surprisingly large number of species. Here the creek, augmented by the water from laterals, was 2–8 feet wide, and had a distance of 30–45 feet between the sloping banks, which were 12–15 feet high (fig. 2). The trees were no longer confined to the banks, but also sometimes occupied the floodplain bordering the channel for a distance of a few yards (fig. 3). They were *Ulmus americana*, *U. fulva*, *Acer Negundo*, *Fraxinus lanceolata*, and *Salix nigra*, the last in much fewer numbers than formerly. All the preceding frequently reached diameters of one and sometimes two feet. *Populus deltoides* was also quite abundant, the largest trees being 3–4 feet thick. *Juglans nigra* was found sparingly, only a few well developed trees occurring in the mile transect. Small trees of *Morus rubra* were infrequent. The more favorable conditions were further shown by the extensive growths of *Symphoricarpos occidentalis* and *S. symphoricarpos*, both on the banks and over the floodplains, where thickets 6 feet high were sometimes found. *Ribes gracile*, *Sambucus canadensis*, and *Amorpha fruticosa* were very common in both situations. *Cornus asperifolia*, *Celastrus scandens*, and *Smilax hispida* were less frequent, but *Vitis vulpina* was very common, sometimes with stems 3 inches thick. *Rhus toxicodendron* was common, *Prunus ameri-*

cana less so; *Rhamnus lanceolata* and *Rubus occidentalis* were also found. In no place was the woodland belt more than a few rods wide.

In one portion of the transect, the stream in changing its course had left a south bank, 15–30 feet high, with a small pond near its base. Through this bank there entered a steep sided ravine, the whole offering a protected place for tree growth. On the sides of this ravine, and on the protected north-facing bank was found a scattered growth of *Quercus macrocarpa*, consisting of small trees mostly 5

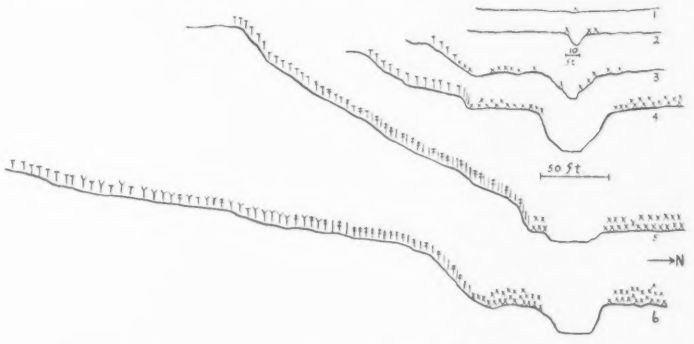

FIG. 3.—Profiles of Weeping Water valley, where transects 1–6 were made: nos. 3–6 show only the south slopes bordering the valley; *X*, floodplain dominants; *T*, bur oak; *l*, linden; ‡, red oak; *Y*, shellbark hickory.

inches or less in diameter, and perhaps 35 feet in height. Associated with it was *Hicoria minima* of similar size, while on the protected lower slope and floodplain were fine specimens of *Celtis occidentalis* and *Gleditsia triacanthos*. *Prunus serotina* was also represented, but by small trees.

Quite in contrast with this area were stretches of the unprotected, windswept valley, which were nearly or quite destitute of woody vegetation. No *Corylus americana* was found, but this occurred quite abundantly along with the oak just northeast of Elmwood.

A fourth examination 3 miles farther down stream and just southwest of Wabash showed further development. Forest growth

extended well over the eighth-mile wide floodplain, which was sometimes bordered on the south by steep slopes 20–50 feet high, covered with upland trees. Dense growths of *Acer Negundo* and *Ulmus* clothed the lowlands subject to overflow. The floodplain forest proper was composed of red and white elm, green ash, walnut, and box elder, and occasionally willows and cottonwoods. Bordering this, especially on steeper banks, were well developed specimens of *Tilia americana*, some 17 inches thick, elms, bur oak, and a little hickory. The oak especially, and the hickory in smaller numbers, spread up ravines and to the crests of hills, forming woodland to a distance of one-fourth mile from the stream (fig. 3). The increasingly favorable growth conditions were revealed in many ways. The floodplain trees were much more abundant, taller, of greater diameter, and the stands were denser. Walnut, ash, and elms, 1–1.5 feet in diameter, were frequent, some of the elms being 4 feet thick. Hackberry, choke cherry, and honey locust, while not abundant, were found scattered throughout, while *Gymnocladus dioica* appeared for the first time. The linden, at first represented by small trees, became 10–12 inches in diameter in more favorable situations. Its range of habitat was very limited, however, being confined to the lower portions of steep slopes (fig. 3). Many of the oaks were 1.5 feet and some 2.5–3 feet in diameter. The wider range of *Ribes gracile* far back from the stream, together with its greater abundance and greater stature, is significant. *Symphoricarpos* spp. formed a shrubby undergrowth, alternating with thickets of *Corylus* in more favored and not too shady situations, and extended beyond the fringing oak forest. These, and *Cornus*, *Sambucus*, *Rhamnus*, *Amorpha*, and *Prunus americana* showed a more vigorous growth, as did also the lianas, *Vitis*, *Celastrus*, and *Rhus toxicodendron*, which sometimes climbed over the shrubs. *Sambucus* was especially abundant. *Rhus glabra* fringed the floodplain forest and extended far into the upland. The following shrubs and vines were also present, the first only in abundance: *Smilax hispida*, *Parthenocissus quinquefolia*, *Xanthoxylum americanum*, *Rubus occidentalis*, and *Clematis missouriensis*. These indicate the rapid development toward true forest conditions.

Four miles eastward the river begins to cut a canyon in the Pennsylvanian (Carboniferous) limestone. Just east of Weeping

Water, 7 miles from the fourth transect, this reaches a depth of 120 feet. Here it is joined by Cascade Creek, also in a small canyon. Taking advantage of the shelter afforded by the rough topography, trees and shrubs have spread widely from the streams, and form a belt of timberland more than a mile wide. Only on the drier, wind-swept southwest slopes does the prairie hold forth, and experimental evidence shows that it is giving way slowly to shrubs and trees (fig. 4). Indeed, the habitat is so diversified that a distinct grouping of the members of the woodland community into associes has occurred. On the floodplains a mixed elm-walnut-ash associes is found; the lower slopes of the canyon banks are clothed with forests of red oak

FIG. 4.—General view of woodland near Weeping Water (transect 5), showing grassland on thin soils overlying limestone on exposed southwest slopes.

and linden; the higher, as well as the protected south slopes, are clothed with bur oak and hickory. The last is fringed on its upper margins with a chaparral community, which extends under the open forest as a more or less suppressed layer. Upon the removal by cutting of any of these forest types (fig. 3), chaparral immediately springs into dominance.

FLOODPLAIN ASSOCIES.—In this transect the floodplain is nowhere over one-third of a mile wide, in fact often less, but much better protected than heretofore. Fine specimens of red and some white elm, walnut, and green ash, 25–50 feet tall and 10 to over 18 inches in diameter dominate (fig. 5). Hackberry, box elder, and wild black cherry also make an excellent growth, while honey locust and Kentucky coffee tree are of less abundance. The chief shrubs are

species of *Symphoricarpos*, gooseberry, wild black raspberry, and elderberry; while grape, smilax, bittersweet, and Virginia creeper are the characteristic vines. All are well developed. The soil of the floodplain forest is not especially rich in humus, since it is subject to overflow, and attendant conditions of aeration or subsequent drought exclude the growth of red oak and linden. Even a slight rise in topography is favorable to these more exacting trees, however, and the floodplain forest often gives way abruptly to them.

RED OAK-LINDEN ASSOCIATION.—*Quercus rubra*, not occurring in the preceding transect, here forms with *Tilia americana* a well defined association. Trees with diameters 8–15 inches and about 50 feet tall are common. The annual precipitation has increased 2 or 3 inches as compared with that at the headwaters, humidity is much higher on these wind protected slopes, and soil moisture is more abundant. Humus is well developed, and rather typical mesophytic forest floor conditions have been attained (fig. 6), *Ostrya virginiana* being the characteristic secondary species. *Ulmus fulva* is common, especially nearer the floodplain, where *Celtis*, *Juglans*, and other floodplain species may occur infrequently. The density of the shade is shown by dead or attenuated bur oaks or hickories, which species flourish farther up the slopes. *Euonymus atropurpureus*, *Staphylea trifolia*, and *Xanthoxylum americanum* occur, with certain other shrubs, but as a whole undershrubs are few and layering is not well developed. The width of this forest community is variable, depending upon the slope, perhaps nowhere over 8 or 10 rods. Just as the lindens grow best on the lower banks, the red oak more nearly dominates farther up the slopes, and the transition to the bur oak-hickory community, although often abrupt, may be quite gradual.

BUR OAK-HICKORY ASSOCIES.—This community was represented almost entirely by open growths of *Quercus macrocarpa*, *Hicoria minima* not being at all important (fig. 7). The trees were usually 6 inches or less in diameter, and only 35–40 feet tall, but excellent specimens were found in favored sites, forming an open woodland. The crowns were rather open. About half the forest was carpeted with *Poa pratensis;* the denser part was covered with a good leaf mulch, the grasses having been shaded out. Aside from a very few scattered hickory and an occasional box elder, with red elm or red

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FIGS. 5, 6.—Fig. 5, floodplain forest of ash, elm, and walnut at Weeping Water; fig. 6, red oak-linden forest on steep north slope.

oak in the moister areas, practically no other trees occurred. *Corylus*, *Symphoricarpos*, *Rhus glabra*, and *Cornus asperifolia* were the characteristic undershrubs, although *Rhamnus lanceolata*, *Sambucus canadensis*, and *Cornus stolonifera* also occurred. The first was found only near the forest margins, or in extensive, dense thickets on cut-over areas. *Symphoricarpos*, often poorly developed, was characteristic throughout; *Cornus* made its best growth in the open places or near the forest margins; while sumac was characteristically a fringing shrub, not enduring the shade well.

CHAPARRAL ASSOCIES.—In the chaparral proper *Corylus* showed its greater mesophytism by occupying the more sheltered areas, although it sometimes occurred on protected hilltops. *Rhus glabra* was more often found on the rocky hilltops and exposed slopes, while *Symphoricarpos symphoricarpos* and *S. occidentalis* occupied a somewhat intermediate position, but showed striking xerophytic tendencies. Associated with these shrubs, especially with the hazel, were *Cornus asperifolia*, *Rhamnus lanceolata*, *Ribes gracile*, *Xanthoxylum americanum*, and various lianas, especially *Celastrus scandens* and *Smilax hispida*, the whole often forming a dense tangle over extensive areas. The shrubs invade the grassland chiefly by their rhizomes and other methods of vegetative propagation. The grasses gradually succumb to these woodland outposts, because of unfavorable light relations, due in part to accumulations of débris. Forests of bur oak may follow in their wake. Thus most of this transect showed continuous woodland cover; ash-elm-walnut forests on the floodplains, red oak and linden on the well protected deeper soils of the north-facing slopes, bur oak in the drier soils above, perhaps with chaparral near and on the hilltops, giving way again to bur oak on the protected lower south-facing slopes, with red oak and linden in the ravines. As a whole the forests are young, however, and grassland often holds forth on the thin soils overlying the limestone on the exposed and windswept south and southwest hillsides (fig. 4).

The next transect was made about 8 miles farther eastward, one and one-half miles beyond Nehawka. Because of its proximity to the forests along the Missouri River, only 6–8 miles farther east, and increasingly favorable growth conditions, the associes were better developed. In fact woodland would undoubtedly be continuous ex-

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FIGS. 7, 8.—Fig. 7, interior of young bur oak forest; fig. 8, floodplain forest of ash, elm, hackberry, and walnut near Nehawka (transect 6).

cept for fires, grazing, cultivation, or other disturbances. The Weeping Water, augmented by numerous tributaries, here assumed the proportions of a rather large stream. The bed is 10–15 feet wide, and in spring and early summer carries a rather large volume of water. Owing to the absence of deep canyons, it has a broad floodplain, extending in places nearly a mile across the valley floor.

The floodplain forest, as before, consisted largely of red elm, ash, and walnut; and hackberry, Kentucky coffee tree, and cottonwoods played an important part. The trees were much taller and of greater diameter than at Weeping Water (fig. 8). Among the dominants a diameter of 16–20 inches was not uncommon, and specimens of elm and hackberry over 3 feet in diameter, breast high, were noted. Fine specimens of walnut logs from this area measured 18–32 inches in diameter, and varied in age from 60 to 170 years. Several specimens of *Gymnocladus* 17 inches thick were found. Other trees characteristic of the floodplain were *Salix nigra*, *S. amygdaloides*, and *Gleditsia triacanthos*, large trees, but rather infrequent; *Acer saccharinum*, *Acer Negundo*, *Prunus serotina*, and *Crataegus mollis*, all rather infrequent.

On higher ground, and especially on north-facing slopes, the floodplain forest gave way to that of red oak and linden. As in the preceding transects, the linden grew best on steeper slopes, where fine, clean boled trees 60 or more feet tall and 10–20 inches in diameter occurred. It was not so limited in its range as heretofore, but extended well up over the gentle slopes, where with red oak it formed a dense forest canopy. Aside from ironwood other trees were rare. The deep litter of leaves and duff covered a rather mellow black soil, filled with fungus mycelia, but supporting only a scant shrubby and herbaceous vegetation of shade enduring species (fig. 9). This forest belt was of variable width, depending upon slope protection. On higher land, the dropping out of the linden was counterbalanced by the appearance of the shellbark hickory, which for a distance afforded a mixed red oak-hickory forest. Higher up the slopes, however, this soon gave way to nearly pure growths of hickory, which covered extensive areas (fig. 10). The trees were mostly 7–10 inches in diameter. This forest was interposed between the red oak-linden association and the bur oak community (fig. 3). Undergrowth

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FIGS. 9, 10.—Fig. 9, well developed red oak-linden forest, with undergrowth of ironwood, near Nehawka; fig. 10, shellbark hickory forest near Nehawka.

TABLE I

OCCURRENCE AND IMPORTANCE OF TREES AND SHRUBS ALONG WEEPING WATER RIVER (*D*, DOMINANT; *S*, SUBDOMINANT; *A*, ABUNDANT; *F*, FREQUENT; *I*, INFREQUENT)

SPECIES	TRANSECT					
	1	2	3	4	5	6
	Trees					
Salix nigra	D	D	S	S	S	S
Salix amygdaloides	D	D	S	S	S	S
Prunus americana	.....	S	S	S	S	S
Prunus virginiana	.....	S	S	S	S	S
Ulmus americana	.....	.....	D	D	D	D
Ulmus fulva	.....	.....	D	D	D	D
Acer Negundo	.....	.....	D	D	S	S
Fraxinus lanceolata	.....	.....	D	D	D	D
Juglans nigra	.....	.....	S	D	D	D
Quercus macrocarpa	.....	.....	S	D	D	D
Populus deltoides	.....	.....	S	S	S	S
Morus rubra	.....	.....	S	S	S	S
Hicoria minima	.....	.....	S	S	S	S
Celtis occidentalis	.....	.....	S	S	S	D
Gleditsia triacanthos	.....	.....	S	S	S	S
Prunus serotina	.....	.....	S	S	S	S
Tilia americana	.....	.....	.....	S	D	D
Quercus rubra	.....	.....	.....	.....	D	D
Gymnocladus dioica	.....	.....	.....	S	S	S
Ostrya virginiana	.....	.....	.....	.....	S	S
Amelanchier canadensis	.....	.....	.....	.....	S	S
Salix interior	.....	.....	.....	.....	S	S
Hicoria ovata	.....	.....	.....	.....	.....	D
Quercus velutina	.....	.....	.....	.....	.....	S
Crataegus mollis	.....	.....	.....	.....	.....	S
	Shrubs					
Symphoricarpos symphoricarpos	.....	A	A	A	A	A
Symphoricarpos occidentalis	.....	A	A	A	A	A
Sambucus canadensis	.....	F	F	A	F	F
Amorpha fruticosa	.....	F	F	F	I	I
Ribes gracile	.....	I	F	A	A	A
Celastrus scandens	.....	I	I	F	A	A
Vitis vulpina	.....	I	A	A	A	A
Rhus glabra	.....	I	F	A	A	A
Cornus asperifolia	.....	.....	I	F	A	A
Rubus occidentalis	.....	.....	I	I	F	F
Smilax hispida	.....	.....	I	A	A	A
Rhus toxicodendron	.....	.....	F	A	A	A
Rhamnus lanceolata	.....	.....	I	F	A	A
Corylus americana	.....	.....	.....	F	A	A
Parthenocissus quinquefolia	.....	.....	.....	I	F	F
Xanthoxylum americanum	.....	.....	.....	I	F	F
Clematis missouriensis	.....	.....	.....	I	I	I
Euonymus atropurpureus	.....	.....	.....	.....	I	I
Staphylea trifolia	.....	.....	.....	.....	I	I
Cornus stolonifera	.....	.....	.....	.....	I	I

in the two communities was not markedly different, although both the shrubby and herbaceous layers were better developed in the bur oak forest, where shade was less dense. *Symphoricarpos* was the chief shrub, although *Cornus* and *Corylus* occurred sparingly. Usually the leaf mulch and shade caused the disappearance even of blue grass, which formed a rather characteristic carpet in more open bur oak forest. The intolerance of the bur oak was often shown by dead trees only a few inches in diameter where the hickories occupied the territory.

Bur oak forest, often with a considerable admixture of bitternut hickory, also covered wide areas. Here, too, the trees were of greater stature than at Weeping Water, but the forest structure was very similar. Chaparral in cutover areas was very well developed. All of the species found in the preceding transect again occurred, usually in increased numbers, and their enumeration for the different communities is quite unnecessary. The almost total absence of *Quercus velutina* was rather surprising. In the better developed forests along the Missouri River southward at Peru, it occupies an intermediate position between the bur oak and shellbark hickory and red oak.

For several miles east of this transect, the widening floodplain has been cleared of timber and the land is cultivated, often quite to the banks of the stream; hence further study was not made. Such a clearing will form a rather effectual barrier to tree migrants up stream. The occurrence and importance of the various trees and shrubs in the several transects are summarized in table I.

Studies along Little Nemaha River

The Little Nemaha has its headwaters (north fork) 2 miles southeast of Cheney and about 10 miles south and 10 miles west of those of the Weeping Water. Its southeastern course roughly parallels that of the latter, approximately 15–20 miles southward.

Conditions in the first transect were practically identical with those already described, *Salix nigra* alternating with *S. amygdaloides*, in a broad valley with practically no channel or merely the beginnings of a ditch.

A second transect, 2 miles eastward, was made across prairie land, where a meandering stream with banks 2–3 feet high was

usually dry in late summer. Low meadow and swamp land about 7 rods wide occupied a part of the area. The dominant tree was *Salix nigra*, which was fairly abundant and 8–14 inches in diameter, but *S. amygdaloides* of equal size was found. *Populus deltoides* was less abundant. *Amorpha fruticosa* and *Sambucus canadensis* were both quite abundant, the former attaining a diameter of 2 inches. *Vitis vulpina*, with a similar stem diameter, was found growing to a height of 30 feet on some of the willows. A single *Ribes gracile* also occurred. A few *Acer saccharinum* and *A. Negundo* had escaped from neighboring groves, as had also one or two *Gleditsia triacanthos* and *Fraxinus lanceolata*. All were small trees. A thicket of *Prunus americana* in a ravine on a neighboring hillside was fringed with *Rhus glabra*, and sheltered a few *Ribes gracile* and *Rubus occidentalis*.

Two and one-half miles eastward and just south of Bennett, a third examination was made. The stream here had a well defined channel, with a depth of 8 feet, with running or standing water, except in the driest times. Because of the gentle gradient, the valley was filled with ox-bow loops, so that from a distance the woodland appeared to be 8 or 10 rods wide. In reality it did not get far beyond the protecting stream banks, which sloped back gradually on depositing shores. A rather precipitous ridge 20–30 feet high bordered the floodplain on the south, and furnished much protection from the wind. *Salix nigra* had entirely disappeared, the dominant floodplain trees being *Fraxinus lanceolata*, *Acer Negundo*, and *Ulmus americana*. Secondary species were *U. fulva*, *Celtis occidentalis*, and *Gleditsia triacanthos*. The shrubs were *Symphoricarpos symphoricarpos* and *S. occidentalis*, about equally abundant. They formed intermittent areas on the lowland and extended well up on the high ridge. Scattered bushes of *Ribes gracile* were common throughout the lowland. *Vitis vulpina*, and to a less extent *Parthenocissus quinquefolia* were rather common. *Amorpha fruticosa* occurred sparingly. A deep, sheltered ravine, extending into the high bordering southern ridge, formed a locally protected area, in which were found *Cornus stolonifera*, *Euonymus atropurpureus*, *Prunus americana*, *Rhus glabra*, and *Rubus occidentalis*, all abundant; and *Clematis virginiana*, *Rhamnus lanceolata*, *Rhus toxicodendron*, *Prunus demissa*, and *Smilax hispida* in smaller numbers. The last was also found on the

floodplain. Near the lower end of the mile transect two small *Quercus macrocarpa* and a single *Juglans nigra* were observed. A mile below, at the junction of the three forks, bur oak was abundant.

A fourth transect was made 2 miles southwest of Palmyra, and about 6 miles east of the third transect. Here the stream had shallow running water 4–8 feet wide during the dry late summer. The rather steeply sloping banks were 8–20 feet high, while the floodplain varied from one-eighth to nearly one-fourth of a mile in width. The lower portion next the stream for a distance of 1–5 rods was subject to overflow, while much of the remainder had been given over to the cultivation of crops. The dominant floodplain trees were red and white elm and green ash, with an abundance of box elder in the more open parts especially subject to overflow. Black walnut and hackberry were both very abundant. When growing in fairly close stands fine specimens of elm, walnut, and hackberry, 50–60 feet tall and from 1 to over 2 feet in diameter, were not infrequent. Thus the dominants had increased one-third to one-half in height. Species of less importance were cottonwood (locally abundant), black willow, and honey locust. Both species of *Symphoricarpos* were abundant everywhere, indicating by their stature much more favorable growth conditions than formerly. Gooseberries, elder, raspberry, grape, Virginia creeper, poison ivy, and smilax were found throughout, all being well developed where the shade was not too dense. Dogwood and burning bush were also widely distributed.

A considerable portion of the floodplain was sheltered on the south by a bank extending 20–40 feet above the general level. Here *Quercus macrocarpa* and *Hicoria minima* formed almost pure stands. Many of the oaks were 6–10 inches in diameter, the hickory being slightly smaller and not getting so far up the hillside as the oak. Beneath the oak and hickory was a well developed layer of *Cornus asperifolia*, *Corylus americana*, *Ribes gracile*, and *Rubus occidentalis*. *Rhamnus lanceolata* was represented sparingly. *Symphoricarpos* spp. and *Rhus glabra* extended from the forest edge to form dense chaparral on the drier upper slopes, which were treeless. A few other trees were found, but none were large specimens. These were *Morus rubra*, *Prunus demissa* (somewhat abundant), *Gymnocladus dioica*, and *Aesculus glabra*. The last two were found in scattered small

clumps only in the most sheltered parts of the forest. Their presence indicated a considerable degree of mesophytism. This was further shown by the invasion of elms, hackberries, and others into the lower slope occupied by the bur oak and hickory.

Upon leaving this area the floodplain gradually widened to half a mile, and then to over a mile in extent, the bordering hills thus usually being far removed from the present tree belt (fig. 11). Two factors had entered to disturb the forests. A drainage channel had been cut in the valley from Syracuse to the Missouri River, a distance of approximately 40 miles, thus leaving much of the old channel dry. The most destructive disturbance, however, had been

FIG. 11.—View along the broad floodplain of Little Nemaha below Syracuse

brought about by the clearing of the forests and the cultivation of the broad fertile floodplain; in fact, it was usually tilled to within a few rods of the stream. Hence much of the remaining vegetation was on land subject to overflow, and only fragmentary sites of oak-hickory were to be found. Extended examination of two transects, the first one mile southwest of Syracuse and another just west of Talmage (which is 25 miles southeast of the Palmyra transect), as well as a third at an intermediate point, showed little change in the floodplain species. As before, elms, ash, walnut, and hackberry were most abundant, with box elders in the newer areas more subject to overflow. Honey locust and willows often played an important rôle. All were nearly or quite as well developed as in the most sheltered portion of the preceding transect, some being even taller and of

greater diameter. Their general distribution over the floodplain, and the greater continuity of the forest, revealed more favorable conditions for growth. This was further shown by an excellent growth of bur oak and hickory on certain south-facing slopes above the floodplain. With these were found all the shrubs and lianas before enumerated as characteristic of the associes. Kentucky coffee trees and honey locusts were much larger than before, as were also the hickories on the higher floodplains. In general, all the shrubs and lianas characteristic of the floodplain had made a much more vigorous growth, a phenomenon especially prominent in bordering plum thickets. *Robinia pseudacacia* was the only new species found, and this was very local, having escaped from cultivation.

The river continues its southeastern course, meandering in a floodplain 1.5–3 miles wide. The land rises without precipitous bluffs to the old dissected loess plain. No extensive tree growth, except that on the uncultivated remnants of the floodplain, was seen for a distance of 10 miles below the last transect. Five miles southeast of Brock, where Rock Creek enters from the north, considerable tracts of undisturbed woodland were found. This stream, with a floodplain one-fourth mile wide, is bordered by hills which rise somewhat abruptly 50–60 feet.

The floodplain forest dominants, as at Weeping Water, were *Ulmus fulva*, *Fraxinus lanceolata*, and *Juglans nigra*. Secondary species and the undergrowth of shrubs were also similar. On the lower, moist slopes bordering the floodplain, a mixed forest of red oak, shellbark hickory, and black oak occurred. Only in limited areas on the longest slopes did a segregation into rather distinct communities occur. These, however, were sufficiently pronounced to show clearly the dominance of the red oak on the best developed, most mesophytic areas. The shellbark hickory, often intermixed with black oak, or the latter forming an upper portion to the black oak-hickory community, occurred above the red oak zone. These trees were 10–20 inches in diameter, and 45–55 feet in height. The higher slopes, even those quite exposed, were clothed with a continuous cover of bur oak and bitternut hickory, the latter being much more abundant than anywhere along the Weeping Water River. Shrubs forming the undergrowth in the woodland and fringing its

borders were of the same species, and quite as abundant as at the Weeping Water station (transect 5). In general, the development of the plant communities, owing to less shelter afforded by the more regular topography, was poorer than at the latter station.

Twelve miles farther down the stream, and only 3 miles from its junction with the Missouri, another favorable place for study was afforded by the meandering stream, with its accompanying floodplain forest, flowing close to the foot of a rather steep north slope. Avoiding undue repetition, it may be noted that here the forest communities were of the same type and of similar distribution to those at Nehawka. The trees and shrubs were fully as well developed, and the black oak, which was rare at Nehawka, here played the rôle of a dominant. Further studies would undoubtedly reveal other woody species along the lower course of the Little Nemaha, but none of any ecological significance.

Discussion and conclusion

From these data it may be seen that a series of wide transects made at carefully selected intervals along the course of a stream reveals in a striking manner the appearance of species in the general sequence of their ecological requirements and their later development into forest communities.

The pioneer trees at the stream sources are those with light, windblown seeds, such as willow, cottonwood, elms, box elder, and ash. Farther down stream, where a floodplain with protecting banks occurs, trees appear which spring from large rodent-carried fruits, such as walnut, bur oak, bitternut hickory, honey locust, etc. The first shrubs and lianas to occur near the stream sources, with the single exception of *Amorpha fruticosa*, all have showy edible fruits which are readily carried by birds. Such are species of coral berry, elder berry, gooseberry, bitter-sweet, grape, dogwood, raspberry, greenbriar, etc. Cherry, plum, mulberry, and hackberry, all appearing relatively early, migrate in a similar manner. Of course the factor of migration, although an essential one, is of little significance unless it is followed by eccesis, that is, germination, growth, and reproduction. Many forest trees, such as linden, red oak, and shellbark hickory, are clearly too demanding in their habitat requirements to pioneer against grasses, and migration alone would be of

little consequence. Chaparral and less mesophytic forests, such as bur oak, regularly precede them in their up-stream invasions.

A study of the sequence of the appearance of trees and shrubby species along stream courses originating in prairie, throws much light upon their ability to tolerate unfavorable growth conditions; for here the balance between forest and grassland is so delicate that a little higher water content, a slightly greater humidity, protection from drying winds, etc., throws the balance in favor of tree growth, while the reverse conditions exclude it. Rate of growth in the several transects, as revealed by width of annual rings, will add much to the story of adaptation to habitat, and form an excellent measure of the growth conditions in the several transects as integrated by the living plant.

At first invaders may appear in mictia, willow, box elder, elm, walnut, oak, hickory, and linden, all in the one rather undiversified habitat, the irregular floodplain. Soon, however, as the stream cuts its channel with a lower floodplain subject to overflow, a higher floodplain, and sloping banks and bluffs, the trees are promptly grouped into definite communities. The intolerant willows largely disappear; box elder clothes the lower floodplain; ash, elms, and walnut cover the upper; and linden, oaks, and hickories are found on the higher ground. Thus a stream course cutting deep canyons has the most diversified forests. One of the most interesting contrasts between the Weeping Water and the Little Nemaha was the rapidity of this early sorting into definite communities in the first, and the much greater distance traversed before this occurred along the latter stream. Well developed bur oak forests were found only 6 miles from the headwaters of the Weeping Water, but 11 miles down the Nemaha. Similarly, the red oak-linden community was well defined 18 miles from the headwaters of the former stream, but down stream a distance of 60 miles on the Little Nemaha.

The behavior of woodland species as revealed by this study, confirms the view that while the woodland along the upper portions of the streams is undoubtedly postclimax, that along their lower course is a part of the generally undeveloped woodland of the subclimax prairie.

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PLANT COMMUNITIES OF ALPINE PARK

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(WITH FIVE FIGURES)

I. Environmental conditions

Alpine Park is situated in Glacier Park, Montana, on the summit of the Lewis Range just south of Logan Pass. The term park is used here in the same sense as elsewhere in the Rocky Mountains, meaning a broad, flat floored valley surrounded by mountain peaks. In this case the park is part of the floor of an upper cirque, which was formed by a glacier which flowed southeast through the valley of Reynolds Creek into the St. Mary's River. Post glacial erosion has reduced the area of the level ground, but it still has an extent of nearly one square mile.

The park is bordered on the north by Mt. Pollock, on the west by Mt. Oberlin and Mt. Clements, and on the southwest and south by the long ridge known as Mt. Reynolds (fig. 1). On the east the ground drops abruptly to the valley bottoms of two mountain streams, which unite to form Reynolds Creek. On the northwest the ring of mountains has been cut between Mt. Pollock and Mt. Oberlin by the recession of the head of Logan (Trapper) Creek Valley, and on the southwest by the cirque which now contains Hidden Lake. The continental divide crosses the park diagonally from Mt. Pollock to Mt. Clements, and then turns back at a sharp angle from Mt. Clements to Mt. Reynolds. This is the result of the cutting back by the valley heads on the northwest and southwest, as a consequence of which the drainage from the northwest and southwest corners of the park flows into McDonald Creek and eventually to the Pacific Ocean. The rest of the run-off waters flow through Reynolds Creek and St. Mary's River to Hudson's Bay and the Arctic Ocean. A small glacier is located at the base of Mt. Clements on the western angle of the divide, so that its flanks extend over into the Pacific drainage area, and on this account it was named Two-

Ocean Glacier by LYMAN B. SPERRY, the pioneer explorer of part of Glacier Park. The water from the central portion of the glacier flows through a shallow valley across the north-central portion of

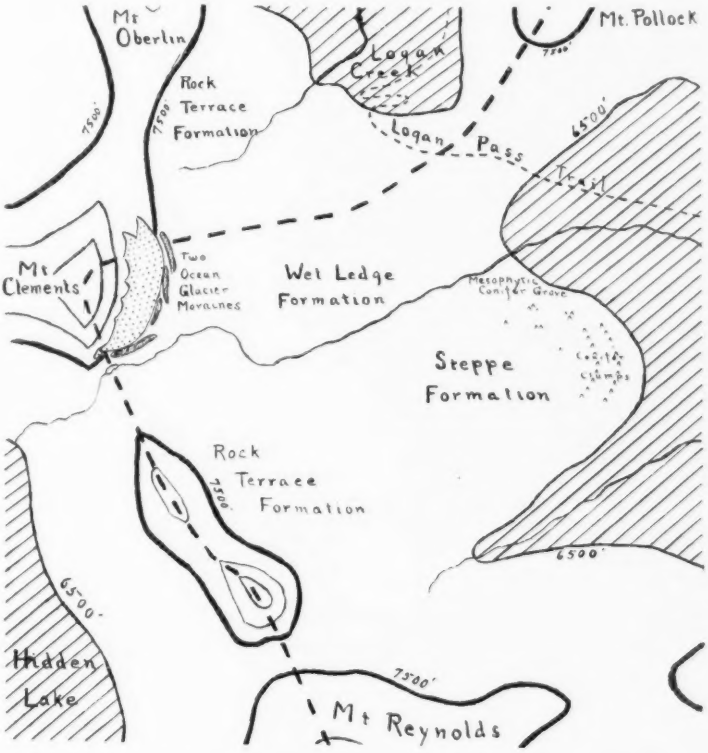

FIG. 1.—Map of Alpine Park: region described lies chiefly between the 6500 foot and 7500 foot contours; areas below 6500 foot contour cross-hatched to bring out area of park; dotted line indicates approximate line of continental divide.

the park, and discharges into a ravine cut between the main level of the park and the slopes of Mt. Pollock on the north. At the southwest corner of the Two-Ocean Glacier is a small pond situated on the divide. A stream flows from either end of this pond, one joining the stream which flows into St. Mary's Valley, the other flowing

into Hidden Lake and thence into the McDonald Valley. On this account the little body of water has been named Two-Ocean Pond.

TOPOGRAPHY.—The eastern portion of the park has a gently rolling topography, controlled by nearly horizontal rock ledges more or less covered by rock waste. On the northeast these ledges lie in concentric curves, but on the south and west sides they are straight, and parallel the bases of the mountains above them. On the west side of the stream valley the ground gradually rises in steps to the slopes of Mt. Oberlin and the moraines of Two-Ocean Glacier. Here the ledges are very marked, and their direction is slightly convex around the base of Mt. Clements. To the north and south of Mt. Clements they become larger and more prominent, and might be called rock terraces rather than ledges.

COMPOSITION OF SOIL.—The soil on the ledges is a thin coating of ground moraine, but in the depressions between them it is black and peaty. The moraines are made up of dry, powdery clay with a large admixture of angular gravel; in fact, they are probably composed partly of surface moraine in which the talus fragments have not been at all worn by glacial friction. There are no bowlder beds such as are found below Grinnel Glacier, owing to the absence of a high surrounding rock wall as a source of such material.

SOIL MOISTURE.—On the east the ledges are relatively dry, but the depressions hold slowly melting snowbanks, and the soil in them is peaty and wet. On the west side the depressions between the ledges are broad, and the dip of the beds is to the southwest, or against the flow of the surface water, so that the waters from the glacier and its surrounding snowbanks keep the soil water soaked most of the time. The rock terraces vary in the amount of water which they receive from above, those at the base of Mt. Oberlin being rather dry, while those on the south side are very wet, and the vertical faces of the terraces are always dripping with water.

CLIMATIC CONDITIONS.—The average elevation of the park floor is about 7000 feet above sea level, and it is always exposed to winds from the west and north, thus insuring a relatively low average temperature. This causes the moist air which flows up from the valleys to condense no matter what the direction of the wind, so that fogs are frequent and general conditions are cool and humid.

II. Plant communities

The vegetation of the park may be divided into four physiographic formations: (*A*) a relatively dry steppe, or coniferous savannah, on the eastern plateau; (*B*) a hydrophytic formation on the wet ledges of the western portion of the park; (*C*) a pioneer formation on the moraine of the Two-Ocean Glacier; (*D*) a formation of the rock terraces north and south of the glacier. In describing the content of the plant communities, there has been no attempt to make exhaustive lists of species, as this study was primarily

FIG. 2.—General view of eastern steppe formation, showing curved lines of conifers governed by buried ledges.

genetical rather than morphological. Chief prominence has been given to the dominant species, and to those regarded as of genetic importance. The seasonal aspect described is that of early and midsummer, and for that reason relatively less attention could be given to grasses and composites. The nomenclature throughout is that of RYDBERG'S *Flora of the Rocky Mountains and adjacent plains*.

A. EASTERN STEPPE FORMATION

East of the shallow central stream valley the ground is rolling and relatively dry, and is covered by a grass formation dotted with scattered clumps of evergreens (fig. 2). This steppe vegetation contains at least four distinct types of community, whose composition

is determined largely by ground conditions. These are: (1) communities of snowbank depressions; (2) communities of the open steppe; (3) xerophytic conifer clumps; (4) mesophytic conifer groves.

1. COMMUNITIES OF SNOWBANK DEPRESSIONS.—These depressions are usually long shallow troughs, which are filled with snow until late in June or the middle of July. In them the soil is gravelly, with considerable humus, and is fairly wet although not saturated. In the bottoms of the troughs the plants are chiefly grasses and sedges, of which *Poa alpina*, *Carex Tolmeii*, and *Juncoides parviflorum* are the most prominent, together with *Claytonia lanceolata*. On the sides of the depressions the *Claytonia* becomes scanty, and its place is taken by *Erythronium grandiflorum*, which grows profusely in these localities, and frequently forms almost pure colonies in close stand. Here, as elsewhere in the mountains, *Erythronium* comes up early, even pushing its way through the snow and blossoming before it has melted away. *Claytonia*, on the other hand, does not appear until the snow has completely left the ground. When the snow first melts, the grasses are dead and dark in color, but later they dominate the bottoms of the depressions, while the spring flowering plants become practically invisible.

2. COMMUNITIES OF OPEN STEPPE.—On the low ridges and level tracts between the snowbank depressions is found the characteristic steppe vegetation. This consists chiefly of grasses and sedges, with local colonies of *Phyllodoce empetriformis* and *P. glanduliflora*, *Salix petrophila*, and *Dasystephana calycosa*. There are also scattered individuals of many species of mountain plants, of which the most prominent are *Erythronium grandiflorum*, *Castilleja* sp., *Dodecatheon pauciflorum*, *Pedicularis bracteosa*, *Veronica Wormskjoldii*, *Sibbaldia procumbens*, *Pulsatilla occidentalis*, *Valeriana sitchensis*, *Pectianthia Breweri*, *Micranthes Lyalli*, *Hypericum Scouleri*, and at least one undetermined species each of *Potentilla*, *Geum*, *Antennaria*, *Arabis*, *Ranunculus*, and several composites. On the drier elevations the ground cover is scanty and open in stand, and the occasional bowlders and patches of bare rock have a scanty growth of crustose lichens.

3. ISOLATED CONIFER ASSOCIATIONS.—The conifer clumps of the east side contain a few trees each, varying from 4 to 20 feet in height,

surrounded by a narrow zone of shrubs and herbaceous plants. The trees grow in close stand and form such a dense tangle that usually there are no ground plants under them. The tree species are *Abies lasiocarpa* and *Picea Engelmanni*, with an occasional pine (probably *Pinus albicaulis*). The narrow shrub zone is made up mostly of *Vaccinium membranaceum* and *V. scoparium*, with some *Dasiophora fruticosa* and occasional specimens of the taller and more vigorous steppe plants. These clumps grow on a dry substratum, in which the soil is thin and sandy, and the underlying rock near the surface. They are either round or oval in shape, or else elongated into long strips or belts. The outlines of the clumps seem to be determined by the topography of the underlying rock, as the trees grow only where the rock is near the surface. Over long ledges of rock the clumps are linear in shape, while the oval ones are found over isolated knobs or hillocks of rock. The rock foundation of the northeast corner of the plateau was originally rounded by erosion, so that the ledges have a semicircular, concentric arrangement. These are covered by a thin layer of soil, but the underground topography is clearly indicated by the arrangement of the rows of conifers (*fig. 2*).

4. MESOPHYTIC CONIFER GROVES.—On the north side of the eastern plateau the ground slopes toward the gulch which borders it on the north. Here the exposure is less extreme, and consequently the trees are larger, the groves more numerous, and the undergrowth assumes a more mesophytic character. The clumps of trees are close together and in some places almost continuous, and the spaces between are occupied by thickets or small meadows. The trees and shrubs are the same species as those found in the isolated conifer clumps, but they are larger and show a better vegetative growth. The ground plants include many of the steppe species, especially *Castilleja* sp., *Erythronium grandiflorum*, *Pedicularis bracteosa*, and *Dasystephana calycosa*. In addition are found such mesophytic species as *Veratrum Escholtzianum*, *Thalictrum megacarpum*, *Viola glabella*, *Heracleum lanatum*, and *Xerophyllum tenax*.

B. WET LEDGE FORMATION

West of the stream which bisects the park, environmental conditions are very different. The ground rises in broad steps to the

slopes of Mt. Clements and Mt. Oberlin, and on these the snow lasts much longer, owing to the protection of the mountain peaks to the west (fig. 3). The soil is soggy with water, and there are very few stretches of the dry steppe which characterizes the eastern section. The drier portions resemble the snowbank depression of the east side, and the characteristic plants are *Erythronium grandiflorum*, *Claytonia lanceolata*, two species of *Phyllodoce*, and *Salix petrophila*. Most of the ground is covered by a formation resembling a wet Arctic tundra. The little streams and ponds are bordered by dense

FIG. 3.—Wet ledge formation on west side of park, below Two-Ocean Glacier

mats of hydrophytic mosses, with some of the more hydrophytic species of the east side and some species not found on the east. Among the steppe species are *Claytonia lanceolata*, *Pedicularis bracteosa*, *Veronica Wormskjoldii*, several saxifrages, and *Pulsatilla occidentalis*. Among those not found on the east side are *Kalmia microphylla*, *Anticlea elegans*, *Mimulus Langsdorfii*, *Pyrola secunda*, and *Tofieldia palustris*.

In one spot a little patch of Arctic muskeg contained *Sphagnum* and the rather rare heather, *Cassiope Mertensiana*. This is a close relative of *C. tetragona*, which is so characteristic of the Arctic barren lands that its woody stems often furnish the only fuel available for

Arctic travelers. The Rocky Mountain species is found only in isolated spots through the western mountains, and, so far as known, has not previously been reported in Glacier Park. The *Sphagnum* also has not previously been reported at this altitude in Glacier Park, although it is found in large bogs above the head of Lake McDonald on the west side of the divide. The only community of this type was found along the stream which flows from the northeast end of Two-Ocean Pond, but it seems likely that others could be found in this portion of Alpine Park. It is probable that its presence there may be explained by the cold wet conditions to be found below the sheltered snowbanks under the slope of Mt. Clements.

C. Communities of two-ocean glacier moraines

Two-Ocean Glacier is located at the base of the eastern cliff of Mt. Clements. Its general shape is that of a slender crescent with a long curving front, and a serrate collecting surface, with points extending up the side of the mountain. The moraines border the front in two rows, and are steep, disconnected ridges of dry, powdery clay with a large admixture of angular argillite. The inner moraines are the younger, and on them there is almost no plant life to be found. The few plants present occur as individuals widely separated from one another, and generally stunted in habit. The species include two or three grasses, of which *Poa alpina* seems to be the first to appear, followed by *Juncoides parviflorum* and *Carex Tolmeii*, together with *Papaver pygmaeum*, *Silene acaulis*, *Pentstemon ellipticus* and *P. virens*, *Epilobium anagallidifolium*, a chickweed, and two composites, probably *Arnica* and *Erigeron*.

On the next line of moraines the plants are found in small clumps about one foot apart, and include the species found on the first moraine with a few additional ones. Among these may be noted *Valeriana sitchensis*, a white *Phacelia*, an *Antennaria*, a dwarf *Taraxacum*, and at least one specimen of *Polystichum Lonchitis*.

D. Rock terrace formation

On either side of the Two-Ocean Glacier the moraines taper out on the wet ledge formation, but farther north and south are found rock terraces, which are formed by the outcropping of the strata in the bases of Mt. Oberlin on the north, and a spur of Mt. Reynolds on

the south. These strata dip slightly to the west, so that their outer edges are higher than the inner, and are consequently dry, with a shallow depression at the base of the terrace next above (fig. 4). The vertical faces of the terraces range from 6 to 10 or 12 feet in height, while their level surfaces are from 10 to 20 feet in width. The outer edges generally carry a narrow belt of stunted evergreens of the same species as those of the clumps on the steppe. The character of the vegetation of the shallow inner trough varies with the amount of water collecting there. In very wet localities the com-

FIG. 4.—Rock terraces southeast of Two-Ocean Glacier

munities resemble those of the wetter portions of the main plateau. Hydrophytic mosses, sedges, and grasses predominate, with *Gentiana*, *Pedicularis*, saxifrages, the two species of *Phyllodoce*, and occasionally *Claytonia* and *Pulsatilla*.

On the drier border between the trough and the conifer belt, and also in the troughs which contain little water, the ground cover is continuous, and resembles the vegetation of the dry steppe. The vertical face of each terrace is usually dry, and xerophytic mosses, crustose and foliose lichens, grasses, and such flowering plants as rockcress, chickweeds, and one or two saxifrages grow in crevices and pockets of the rock face.

When the water from above is abundant, it trickles down over the face of the terrace, and the vegetation is more luxuriant and mesophytic, or even hydrophytic. Mosses are abundant, with lichens and some ferns, and even liverworts. Among flowering plants are *Thalictrum megacarpum*, *Saxifraga* spp., *Viola glabella*, and local colonies of the rare *Romanzoffia sitchensis* and *Pinguicula vulgaris*. Farther from the glacier the terraces gradually disappear, and the vegetation takes on the form found regularly on valley walls and upper mountain sides.

III. Development of plant communities

A region occupied by retreating glaciers is one of the few spots on the earth's surface affording evidence as to the order of development of vegetation on clay as well as on bare rock. A comparative study of the communities in Alpine Park should furnish some information as to the composition and order of the successive communities which have appeared in these valleys and on the mountain sides.

A general survey of the various communities found in this region would indicate that the climax community, under present conditions, is the heavy conifer forest found in the river valleys of the east front. The forest of the McDonald Creek Valley is even more luxuriant, but it also contains many Pacific Coast species which are not found east of the divide on the crest of the Lewis Range. The exact relationship of these two forests cannot be stated definitely, until more is known of the general relationship of the Rocky Mountain and the Pacific conifer forests. For this reason, only the succession of the vegetation of the east slope will be considered here.

As one leaves the heavy forest on the valley floor and ascends the slopes, the trees are found to be more open in stand and more xerophytic in character. Thickets and mountain meadows appear in gaps in the forest, and they become more extensive as the timberline region is approached. The glacial moraines are usually found just below timberline, and are generally bordered by exposed rock terraces and ledges, which characterize the bases of the adjoining mountain.

In this region the progressive changes in vegetation which were vertical on the valley sides, now become horizontal. The trees take on timberline characteristics, and are stunted and scattered, until

they pass into meadow or steppe, and finally into the plantless areas of the youngest moraines. Reversing this order, it will be seen that the latest moraines represent the pioneer habitats of the succession, the rock ledges and upper slopes carry the intermediate stages, and the river valleys the climax stages. Two successions may be followed, one beginning on the mixed clay and gravel of the moraines, the other on the bare rock ledges or terraces.

A. Clay-gravel succession

1. Xerarch.—The pioneer stage in this succession is found in the youngest moraines of the Two-Ocean Glacier. A comparison of photographs taken in 1905, 1919, and 1923 indicates that all the glaciers of Glacier Park receded very little between the first two dates, but retreated rapidly between 1919 and 1923. Apparently the inner moraine was at least partly covered in 1919, and so the scanty vegetation found on it has come in since that date.

The first pioneer plants thus seem to appear on the dry moraines within a few years after the melting of the ice. The absolute pioneer is *Poa alpina*, and a few flowering plants such as *Papaver pygmaeum*, *Silene acaulis*, two species of *Pentstemon*, *Epilobium anagallidifolium*, a chickweed, and two composites. The individual plants are widely separated, stunted in size, and grow very slowly. They increase rather slowly in size and in number of stands, as indicated by the conditions observed on the second moraines. So far no attempt has been made to set a date for the uncovering of this line of moraines, as little is known of the rate of recession of these glaciers previous to 1900. The rate of invasion by the plants of the secondary stages can be estimated only in a very general way.

On this outer line of moraines the grasses and sedges have increased in importance out of proportion to the other plants, and the composites also have increased in number and area covered. On the whole the vegetation is denser at the ends of the line nearest the flanking mountain slopes, and representatives of conifer species have begun to appear. It was in this part of the moraine that *Polystichum* was found. There are no conifers on the moraines of the Two-Ocean Glacier, but in similar situations on the moraines of other glaciers in Glacier Park small clumps of conifers are found on the

outer edges of the older moraines. These are usually tree species, chiefly alpine fir, Engelmann spruce, and whitebark pine, but *Juniperus sibirica* is frequently associated with them. They are all extremely stunted in habit, and are located either in slight depressions or on protected slopes of the moraine ridges. The clumps seem to increase in size very slowly, and do not show any tendency to cover the ground completely. From these facts it would appear that the plants of the secondary stages have migrated slowly from the communities already established on the adjoining mountain sides, rather than from the steppe below.

As the moraines are generally separated from the steppe by the wet ledge formation, it is difficult to determine the relationship between the two, but apparently the steppe represents a temporary climax on a dry clay-gravel substratum. The conifer groves on the steppe do not seem to be increasing in size, and as they are definitely connected with buried rock ledges, it would seem as if they early became established on these dry spots and have not been able to advance over the grass mat of the steppe. The fact that the groves are more mesophytic on the sheltered northern slope of the plateau, might indicate that under favorable conditions they increase in size and eventually cover the whole area.

2. HYDRARCH SUCCESSION ON CLAY-GRAVEL.—Glacial ponds show no traces of the earlier stages of the regular aquatic succession. These waters are clear and plantless from the center to the edge of the surrounding land, and the banks, although low, generally have vertical faces at the water's edge. The absence of aquatic plants is probably due to the short ice-free period and the very cold water. Even if the plants could grow in the cold water, the supply of seeds would be very scanty on account of the high gradient of the outflowing streams and the small numbers of aquatic birds which visit them from the valleys. In the small ponds and troughs and the narrow streams which flow from them, the pioneer plants seem to be hydrophytic mosses of the hypnum type, and rarely sphagnum. These form dense water soaked cushions, under which a sort of peat accumulates. In this wet substratum the first flowering plants to appear are usually *Saxifraga Lyalli* and *Pedicularis bracteosa*, followed by *Phyllodoce* spp., *Kalmia microphylla*, and the other species

already noted. The *Sphagnum-Cassiope* association is found only in isolated patches, and there was no evidence to show whether or not it constitutes a stage in the succession (fig. 5). Apparently it is contemporaneous with the hydrophytic communities with which it is associated, but only a microscopic examination of the underlying peat deposits could establish this point.

The progress of the development on the borders of these ponds and streams is very slow, but the wet meadow or snowbank depression communities apparently invade the peat beds as the substratum

FIG. 5.—Two-Ocean Pond; *Sphagnum-Cassiope* association found a few hundred yards to right of this pond.

becomes drier, and the open steppe formation would seem to be the temporary climax of the hydrarch succession, under present climatic conditions.

B. ROCK SUCCESSION

1. XERARCH.—The pioneer plants on bare rock surfaces are crustose lichens, ranging in color from black and white to brilliant yellows and reds. These are abundant on both vertical and horizontal surfaces near the mountain summits, and they also occur frequently at lower levels. This pioneer stage seems to continue for long periods of time with very little change, as lichen covered rocks

are to be found even among conifer groves. This is probably due to the small amount of dust present, and also to the washing effect of the frequent rains. For these reasons soil does not accumulate around the lichens, and plants of the later rock stages are unable to get a foothold. Where advanced stages of vegetation are found on a thin layer of soil over rock, the character of this soil makes it seem probable that it was left there after the retreat of the ice, rather than that it accumulated in connection with the development of vegetation. Where the rocks have cracks or pockets, crevice plants have become established, and even stunted conifers may be found. Even here, however, the development has not advanced on the rock, as there is little extension of the vegetation beyond the limits of the soil holding pockets.

2. HYDRARCH.—In rock troughs and shallow basins in which water stands throughout the summer, development has usually made some progress. The miniature pond will usually be bordered by a zone of hydrophytic mosses, sometimes equalling or exceeding in width the relict pool in the center. This moss carpet will be underlain by a layer of peat, the thickness of which will depend on the topography of the rock and the distance from the center of the pool. The deposit of peat will naturally become thinner toward the edges of the original pool, except where local depressions in the rock held secondary pools around the edges of the main body of water.

In the moss cushion growing above this peat, a few angiosperm species have become established. These hydrophytic pioneers include *Saxifraga Lyalli*, *Pedicularis bracteosa*, and *Tofieldia palustris*, but as the peat becomes drier, other members of the wet clay-gravel meadow invade. As the rock ledges around these ponds generally carried a clay-gravel deposit, a careful examination of the substratum is necessary to determine whether these secondary stages have developed on peat or on morainic soil. Of course in cases where the peaty character of the soil is established, these stages may be regarded as truly belonging to a rock succession, but in a majority of cases the development on peat appears not to have progressed very far. These observations, taken with hints from other localities, make it seem probable that the development of advanced stages of a cycle is relatively rare on a bare rock substratum. The progress of suc-

cession on bare rock is so slow, that unless it can be demonstrated that a peat soil extends quite to bed rock, it seems probable that the later stages have developed over morainic material rather than over rock.

On vertical rock surfaces over which an abundance of water is always flowing, a hanging curtain of hydrophytic mosses may develop. This will reach considerable thickness on miniature ledges and in pockets, and here also the pioneer hydrophytic angiosperms of the horizontal moss carpet will be found.

Summary

1. The area described is located near Logan Pass in Glacier Park, Montana, and consists of a level tract about one mile square between mountain peaks, at an average elevation of 7000 feet.

2. Four physiographic formations were found: a grassy steppe dotted with clumps of conifers, a wet Arctic meadow between low rock ledges, a glacial moraine formation, and a rock terrace formation.

3. The xerarch succession of these communities proceeds from pioneer stages on the glacial moraines, to grass steppe dotted with conifer clumps. The steppe seems to represent a temporary climax, with the conifers as a possible later stage under more favorable conditions.

4. The hydrarch succession develops in ponds left by the melting glacier, but does not proceed further than a wet meadow stage.

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COMPARATIVE MORPHOLOGY OF CYTOPLASM AND CHROMATIN

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 339

CHARLES J. CHAMBERLAIN

(WITH PLATE XII AND THREE FIGURES)

A study of the eggs of various cycads, even with the technique of twenty years ago, indicated that they furnish unusually good material for an investigation of the structure of cytoplasm, just as the Cucurbitaceae furnish unusually good material for a study of sieve tubes; while a study of chromatin, especially in root tips, with graduate students, raised the question whether the structure of cytoplasm and chromatin may not be fundamentally identical. The accumulated impressions from studies with classes, together with the writer's own investigations, have prompted the assembling of the results and the drawing of some conclusions.

Cytoplasm

The eggs of cycads are the largest in the plant kingdom, reaching a length of 6 mm., with a diameter of 2 mm. Although very small, compared with the eggs of the bird *Aepyornis*, which reach a length of 30 cm. with a diameter of 20 cm., or even when compared with the eggs of living birds, like the ostrich or emu, it may be doubtful whether these enormous eggs had nuclei as large as the egg nucleus of *Dioon edule*, which sometimes reaches a diameter of 500 μ.

The cytoplasm of the cycad egg, or central cell as it is called, is extremely vacuolated before the mitosis which results in the formation of the ventral canal nucleus and the egg nucleus, because it increases immensely in volume without much increase in the mass of cytoplasm. Some of the vacuoles are so large that they can be seen with the naked eye, but as the egg approaches maturity, a nutritive jacket develops about it, the cytoplasm increases rapidly, and the vacuoles disappear, until at the time of fertilization not many vacuoles can be seen with a high power dry lens.

Most of the investigations upon the structure of cytoplasm have been made by zoölogists, who have formulated various theories, notably the framework theory of FROMMANN, the filament theory of FLEMMING, the granula theory of ALTMANN, and the foam theory of BÜTSCHLI. E. B. WILSON'S investigations upon echinoderm eggs proved conclusively that cytoplasm is an emulsion, and gave such strong support to BÜTSCHLI'S theory that it has become generally accepted. According to BÜTSCHLI, there is a groundwork consisting of an immense number of closed spaces filled with watery liquid. The diameter of the spaces is usually less than a micron. WILSON found larger spaces, up to 3–4 μ in diameter. STRASBURGER had described some small spaces, but also some much larger spaces, which BÜTSCHLI claimed did not represent the real structure of cytoplasm, although he admitted that STRASBURGER occasionally got glimpses of the real structure.

In dealing with paraffin sections, technicians know that it is easier to get good preparations from animal than from plant tissues. This is because the vacuoles, or alveolar spheres in animals are so small, usually only 1–3 μ in diameter, while in plants the vacuoles are usually much larger. In the sporogenous tissue of plants, in spermatogenous tissue, in embryos, in meristem, and also in the whole group of Cyanophyceae, where the vacuoles are as small as in animals, the technique is easy; but in embryo sacs, endosperm, and most plant cells, where the vacuoles are very large, the technique is difficult.

This study of the cycad egg endeavors to show that there is an unbroken series, from large vacuoles 100 μ or more in diameter, down to the smallest spaces demanded by the theory of BÜTSCHLI and WILSON, and that the largest and smallest spaces are of the same morphological nature. Then, in the study of the chromosomes of the root tip and microspore mother cell, I shall try to show that the structure of the chromatin is only such a modification of the structure of the cytoplasm as should be anticipated if the chromatin has been derived, phylogenetically, from the cytoplasm. This involves the supposition that the original living matter was not differentiated into chromatin and cytoplasm, that differentiation having come later.

A complete series of stages showing the condition of the cytoplasm during oogenesis of a cycad should begin with the archesporial cell (if there is such a cell in cycads), or at least with the megaspore mother cell; but, so far as I know, only three persons have ever secured preparations of that megaspore mother cell. F. GRACE SMITH finally found it in *Zamia floridana* by going to Miami where the plant grows; TREUB found the megaspore stage in *Ceratozamia;* and LANG found the same stage in *Stangeria*. The fact that cones are covered in the bud during early stages in oogenesis makes it practically impossible to secure material in greenhouses.

During these early stages any vacuole would be very small, for the entire megaspore mother cell could not have one-fiftieth the length of a mature egg. Stages in the development of the female gametophyte show that the vacuoles increase rapidly in size until the central cell reaches its maximum length of 3–6 mm.

Most of the illustrations are chosen from *Ceratozamia mexicana*, beginning about fourteen weeks before fertilization. At that time the central cell has the appearance shown in the photomicrograph (fig. 1), and the drawing of another section of the same cell (fig. 4). The size of this cell is enormous, as compared with the surrounding cells, which are about as large as the original archegonium initial; but the increase in mass of cytoplasm has not kept pace with the increase in the size of the central cell.

No attempt was made to determine the chemical nature of the liquid in the vacuoles, but at this stage it is almost watery in consistency, and the big cell is extremely turgid. If, in trimming material for fixing, the blade comes too near the central cell, liquid spurts out so violently that it can be felt at a distance of several centimeters. This extreme turgidity continues throughout the development of the central cell and egg, and even after fertilization, until the mass of cytoplasm begins to be absorbed by the growing embryo.

The largest vacuole shown in figs. 1 and 4 has a diameter of 150 μ, but the smaller vacuoles are of the same morphological nature. Under greater magnification the cytoplasm between vacuoles, which appeared to be nearly homogeneous under the lower power, shows a series of vacuoles of various sizes down to the limit of vision (figs. 2.

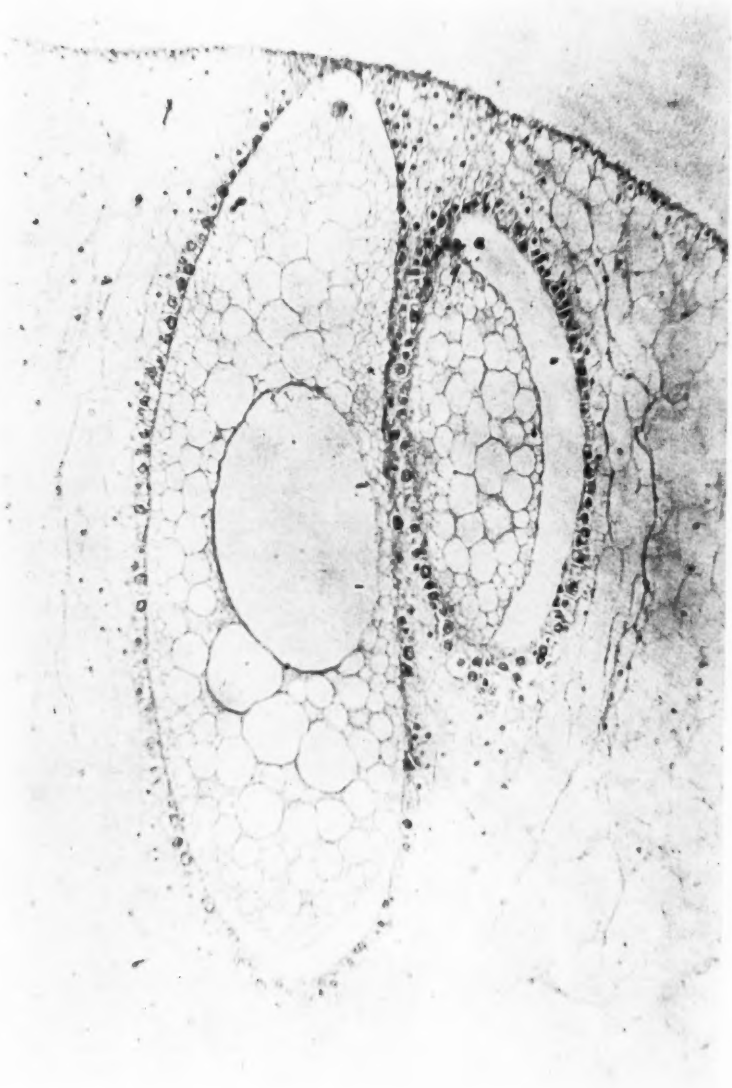

FIG. 1.—*Ceratozamia mexicana:* central cell about 14 weeks before fertilization; ×100.

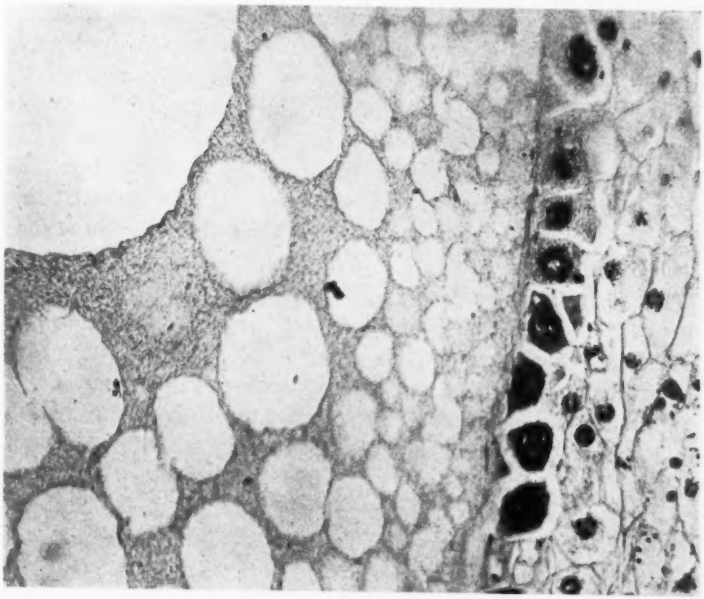

FIG. 2.—*Ceratozamia mexicana:* central cell 10 weeks before fertilization; ×847

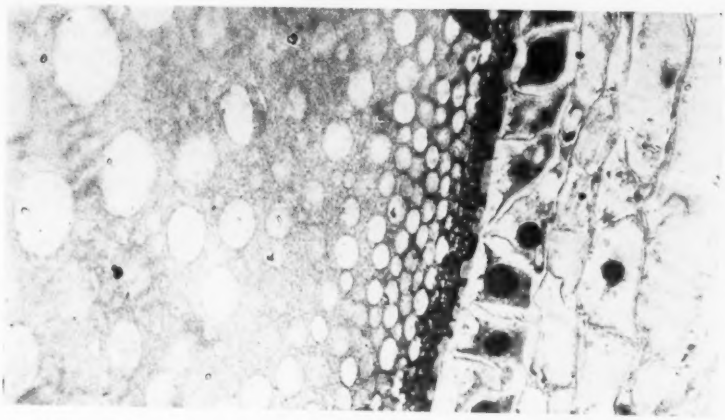

FIG. 3.—*Ceratozamia mexicana:* central cell 8 weeks before fertilization; ×613

5). With a Zeiss 2 mm. apochromatic objective, 1.4 N.A., and a 15× compensating ocular, vacuoles much less than 1 μ in diameter can be recognized (fig. 5). It is probable that if a much higher efficient magnification could be obtained, still smaller vacuoles would become visible.

During these early stages in the growth of the central cell, it is thought that the vacuoles are alike morphologically, and that their contents are more or less uniform; but as the endosperm becomes packed with starch and various materials, the central cell develops its large haustoria and takes in substances of various kinds. Among these are proteids, which often take a crystalloid form. All cycads contain poison. It may be that some of the globules and irregularly shaped masses constantly present in the endosperm during the later stages of its development are the poisonous material, and it is possible that some of the vacuoles of the eggs in its later stages become filled with the poison.

At a stage even earlier than that shown in fig. 6, about two months before fertilization, globules which stain deeply with safranin and iron haematoxylin appear in the central cell. Morphologically they are not different from the substances which filled the other vacuoles shown in this figure, but which were dissolved in the preparation for microscopic examination. During the two months which elapse between this stage and fertilization, great quantities of material are taken into the central cell. So long as the walls of the jacket cells remain intact on the side next to the central cell, any material must pass by osmosis (fig. 6); but as the time for fertilization approaches, these walls are broken by the haustoria, and material in masses can pass from the jacket cells to the egg as readily as from one part of the jacket cell to another (fig. 7). Material filling some of the larger vacuoles in the peripheral portion of the egg breaks into large numbers of small globules, as shown in fig. 7, occupying, at first, the position of the large vacuole, and then becoming scattered throughout the egg. The visible vaucoles become smaller and smaller, while the quantity of apparently homogeneous cytoplasm increases.

At the time of fertilization, which occurs a few days after the division of the nucleus of the central cell, giving rise to the egg

nucleus and the ventral canal nucleus, the vacuoles are so small that only a few of them can be seen with a low power dry lens. At the instant of fertilization, cytoplasm breaking out from the egg between the two neck cells shows elongated vacuoles, and gives a definite impression of streaming (fig. 8). As it comes to rest just outside the neck cells, however, the vacuoles are much smaller, and at the periphery of the mass which flowed out, the structure is apparently homogeneous, with no recognizable vacuoles.

In *Stangeria*, at the time of fertilization, the egg contains innumerable small vacuoles. The immense size of the egg nucleus, as compared with the vacuoles, is seen in fig. 10, in which the nuclear membrane (*m*) shows scarcely any curvature. As the free nuclear period in the development of the embryo advances, starch appears in its periphery, probably brought in bodily from the jacket walls through the haustoria.

Until it completes the free nuclear stage, the embryo receives nutrition rather uniformly from all the surrounding cells; but as the cellular stage begins, the embryo breaks through the bottom of the egg, and receives more and more nutrition from that region, while the jacket ceases to furnish material. Soon all the material in the upper part of the egg is absorbed, and its original contour is maintained only by the very thick egg membrane.

Some of the later stages in the cytoplasm of the egg were not studied very carefully, but the structures are certainly developed from the vacuolated condition already described. Shortly before fertilization, it is common to find in the egg considerable areas which have a distinctly thready or reticulate structure. The globules and small granules which become increasingly abundant as fertilization approaches, I regard as contents of vacuoles, of a different character from the contents dissolved out from the rest of the vacuoles.

Chromatin

So far as the actual structure of the chromatin is concerned there is nothing new to add. I simply affirm my belief that the chromatin in plants is a vacuolated substance like the cytoplasm, and that in the plants studied there are no such structures as chromomeres upon a linin ribbon. For many years our classes in cytology have

studied mitosis in various root tips, especially those of *Tradescantia virginica*, *Vicia Faba*, and *Trillium grandiflorum*. The vacuolated condition during telophase, resting condition, and early prophase seems evident. The figures are drawn to the same scale as figs. 5–11, from sections 3 μ thick, stained in iron-alum haematoxylin. A modification of Flemming's weaker solution, with the osmic acid still weaker than in that formula, was used for fixing.

The chromatin from anaphase to late prophase of the next mitosis is vacuolated. The structure is the same as that of the cytoplasm, except that the vacuoles are much smaller, and, since the chromosomes are elongated, are arranged more or less in rows. In places where there is only one row of rather uniform vacuoles, the resemblance to chromomeres on a linin thread is quite pronounced (figs. 12, 13, and right hand part of 14). In the great majority of cases, like the left part of fig. 14 and figs. 15–19, the vacuolization is evident.

Theoretical considerations

It is hardly probable that the original living matter had the familiar complex mitotic arrangement for division. In spite of the fact that many lines of evolution show progressive simplification rather than increasing complexity, it is more probable that the original living matter was comparatively simple and that the differentiation into cytoplasm and chromatin came later. A comparative study of the Cyanophyceae might show stages in such a differentiation.

Definite chromomeres upon a linin ribbon afford a convenient resting place for genes, and facilitate philosophical speculation, especially if a theory demands a rigid serial arrangement of hereditary characters in the spirem. In a vacuolized chromosome there might be some serial arrangement, but it could not be so definite. On the other hand, if the vacuolization theory is correct, as it seems for all the plants I have studied, the chromosomes of early telophase would not be absolutely the same when they reach the next mitosis. Parts of the slender threads might be drawn back into the chromosomes from which they were drawn out; or they might break in such way as to go to the contiguous chromosome, and thus cause more or less variation. We are not dealing with theories, however. It

seems apparent that both cytoplasm and chromatin are vacuolated and of essentially the same structure. We should not claim that such structures as linin and chromomeres do not occur in some animals; but I feel certain that they do not occur in the plants studied, and I predict that theories which cannot be reconciled with a vacuolated structure of the chromosome will have to be abandoned.

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EXPLANATION OF PLATE XII

The photomicrographs, text figs. 1–3, were made by Mr. C. Y. CHANG. Fig. 4 was drawn with a 16 mm. objective and a 6× ocular; figs. 5–19 were drawn with a Zeiss 2 mm. apochromatic objective, 1.4 N.A., and compensating ocular 15×; and all figures, except the photomicrographs, were reduced to $\frac{5}{8}$ the original size. Fig. 4 is magnified 62 diameters; figs. 5–19 are magnified 1250 diameters.

FIG. 4.—*Ceratozamia mexicana:* central cell 14 weeks before fertilization, showing vacuoles of various sizes.

FIG. 5.—*Ceratozamia mexicana:* small portion of cytoplasm of central cell at stage shown in fig. 4; diagram 5*a* shows position of piece selected for the drawing.

FIG. 6.—*Ceratozamia mexicana:* portion of central cell 8 weeks before fertilization, showing thick egg membrane (shaded) and vacuoles of various sizes; parts of three large jacket cells shown at left.

FIG. 7.—*Dioon edule:* portion of egg about the time of fertilization, showing globules which break into groups of smaller globules as they penetrate farther into the egg.

FIG. 8.—*Ceratozamia mexicana:* cytoplasm streaming out between neck cells at fertilization.

FIG. 9.—*Ceratozamia mexicana:* cytoplasm just outside neck cells after escaping from egg.

FIG. 10.—*Stangeria paradoxa:* small vacuoles in cytoplasm at time of fertilization; right hand part of figure shows small portion of egg nucleus; *m*, nuclear membrane.

FIG. 11.—*Stangeria paradoxa:* small portion of embryo in 32-nucleate stage; groups of starch grains (*s*) shown near periphery; small portion of one of the 32 nuclei shown at right.

FIG. 12.—*Trillium grandiflorum:* portion of chromosome in telophase of heterotypic mitosis in pollen mother cell.

FIG. 13.—*Trillium grandiflorum:* somewhat earlier stage than that shown in fig. 12.

FIG. 14.—*Trillium grandiflorum:* telophase of homotypic mitosis in pollen mother cell.

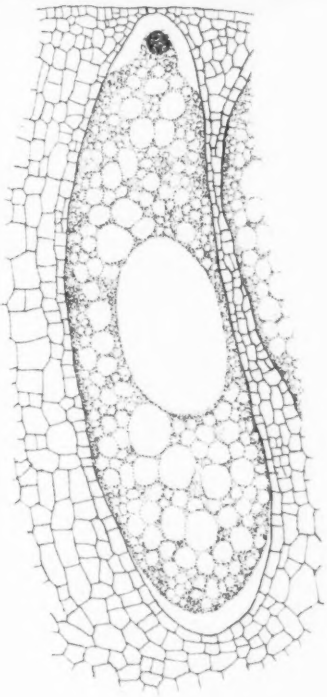
FIG. 15.—*Trillium grandiflorum:* slightly earlier telophase of homotypic mitosis than that shown in fig. 14.

FIG. 16.—*Trillium grandiflorum:* chromosome in telophase of heterotypic mitosis in pollen mother cell.

FIG. 17.—*Tradescantia virginica:* portion of chromosome in prophase in root tip.

FIG. 18.—*Tradescantia virginica:* portion of spirem in prophase in root tip.

FIG. 19.—*Tradescantia virginica:* portion of spirem in slightly later prophase in root tip than that shown in fig. 18.



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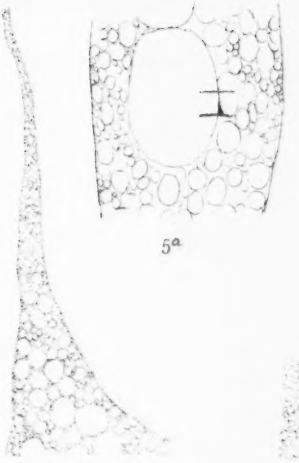

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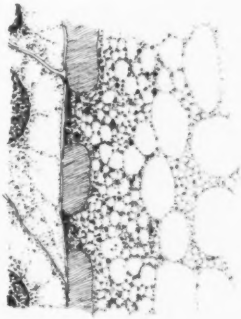

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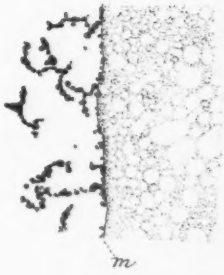

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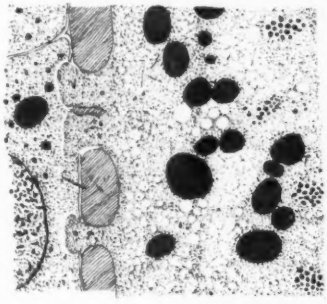

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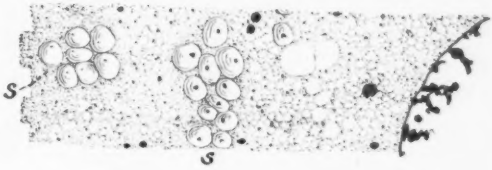

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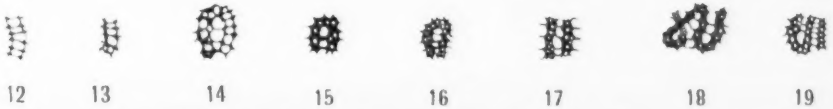

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CHAMBERLAIN on CYTOPLASM and CHROMATIN

VEGETATION OF NORTH GREENLAND

C. H. OSTENFELD

I

As Greenland extends from 60°N. to about 83.5°N., the conditions for vegetative life are very different in its southern subarctic part, where there are copses of birch (*Betula pubescens*), and in the most northern portion, which supports the most northern vegetation. The present paper deals only with the vegetation of North Greenland, that is, Greenland north of 76°N. The botanical knowledge of this part of Greenland has increased greatly during the last two decades, due partly to American explorations, but mostly to the information obtained by Danish expeditions.

Usually Arctic expeditions have included no trained botanists, but one Danish expedition, the Second Thule Expedition under command of KNUD RASMUSSEN in 1916–1918, was an exception. Dr. THORULD WULFF, a well known Swedish botanist, accompanied this expedition, which explored the most northern coast of Greenland facing the polar sea. Dr. WULFF succumbed to the hardships of the expedition as land was reached, after having traversed the inland ice just south of the Humboldt Glacier. He left a small collection of plants, made with wonderful energy under the hardest conditions, and also a diary containing many botanical and meteorological observations.

It has been the writer's privilege to identify the higher plants of this collection and to make use of his diary. The results are embodied in a recently published paper,[1] of which the first part of the present article is to some extent a résumé. It is rather surprising that this flora contains not less than seventy species of higher plants, that is, flowering plants and vascular cryptogams, in spite of the poor conditions under which they live. If we examine the main factors of importance to plant life, we find the following points of interest.

1. In the short portion of the year during which plants are able

[1] OSTENFELD, C. H., The vegetation of the north coast of Greenland, based upon the late Dr. TH. WULFF's collections and observations. Medd. om Grönland **64**: 221–268. 1924. København.

to grow in these high arctic latitudes (82°–83°N.), the sun is constantly above the horizon and consequently the plants are able to assimilate without interruptions due to darkness. From WULFF's observations it appears that during the three months, May to July, when he worked on the north coast, there was much sunshine; he has nearly one hundred meteorological observations for each month and about half of them report sunshine, while there are very few notes about fog or mist (hardly 10 per cent of the observations).

2. The temperature is not favorable. According to WULFF's observations, the air temperature during the three months shows that in May it never reached the freezing point, in June the mean temperature was about zero (C.), and not until July was there a

TABLE I

TEMPERATURES (C.) FROM WULFF'S OBSERVATIONS

Month	No. of observations	Mean
May	93	−8.7
June	110	−0.1
July	100	+2.65

mean temperature above the freezing point (table I). There are observations only for the first three days of August, but if we take observations from other arctic places into consideration, we may conclude that the mean temperature is not much above zero, most probably near to it (table II). This means that the plants have only one month in the year in which they really grow, taking for granted that the flowering plants are not able to grow at temperatures below freezing. It must be borne in mind, however, that the plants absorb heat from direct insolation, and thereby get temperatures decidedly above that of the air. WULFF made several experiments to show this. He found such differences as the following: air temperature (May 19) −11.8°C., while the temperature in a tuft of moss was 9.2°C.; air temperature (June 20) −5°C., and that of a flowering tuft of *Saxifraga* 21.1°C. This of course is of importance for the plants, but if we compare his observations with others of the same kind from arctic regions of lower latitude, we find that the difference between the air temperature and that of plant tufts is less than we should expect.

3. The precipitation according to WULFF is rather inconsiderable in the summer, and most of it comes as snow, except in July. The air is very dry in the first part of the summer, and the evaporation in the uninterrupted sunshine is rapid. The snow evaporates so quickly that it disappears without making the ground wet. The plants, therefore, are liable to suffer from lack of available water, in spite of the apparent abundance of snow and water. The frozen soil intensifies this condition, and not before the rains and snow melting of late summer do plants get sufficient water.

TABLE II

MEAN TEMPERATURES (C) IN SOME HIGH ARCTIC REGIONS

Region	Latitude N.	May	June	July	August	September
Frans Joseph Land (Cape Flora)	79°56′	−8.5	−9.4	1.3	0.2	−4.0
Danmark Harbour, Northeast Greenland	76°46′	−8.2	−1.1	3.3	2.3	−4.4
Fort Conger, Ellesmere Land	81°44′	−8.1	0.6	2.7	0.8	−11.7
North coast of Greenland	82°83′	−8.7	−0.1	2.65	?	?

4. Air movements seem rather favorable. Only ten out of WULFF's three hundred records indicate a force of wind over 5 of the Beaufort scale, and one-half of his observations report no winds. At other seasons surely strong winds are much more common, but then most of the vegetation is covered by snow.

5. This snow covering is an important factor for the protection of plant life in these regions, and not until the middle of June does the melting reach any considerable extent, and at the end of July the snow begins to reappear. Thus the ground is bare only between one and two months, and in many places the snow melts off only during the most favorable years.

6. There are few data regarding the soil. Most of the surface soil of the north coast is loose, coming from a substratum of Devonian sandstone. The rapid disintegration forms a loose surface, consisting of stones and gravel, with finer elements (clay) between. In some places the melting snow and the streams produce a clayey soil, in others the stones prevail. The so-called "polygon-field" is very common on horizontal surfaces, consisting of a network of

fissures formed by the drying up and cracking of the soil. The vegetation is usually confined to the fissures, while the surface itself is bare. Another kind of soil peculiar to arctic and high alpine regions is that due to solifluction (or slumping), occurring on sloping ground during the melting of the snow when the surface soil attains a consistency resembling porridge, while the subsoil remains frozen. A slow motion is set up in the surface soil, due partly to the slope and partly to the steadily increasing water supply. This movement is comparable with that of a lava, and by it small stones are arranged in curved lines at right angles to the direction of flow. Such a phenomenon, of course, is quite unfavorable to plant growth, and is common on the Greenland north coast.

This summary of the factors governing plant life shows how difficult the conditions are for the plants. The vegetation is always very low and close to the ground. Usually the individuals stand scattered, and only on specially favorable places do continuous mats of flowering plants, mosses, and lichens occur. All the species of higher plants are perennial, as the short time of growth does not allow annuals to exist. They develop either as herbs or as dwarf shrubs, classed according to RAUNKIAER's biological types as hemicryptophytes and chamaephytes, the latter being well represented and characterizing arctic as compared with temperate vegetation.[2] Growth during the short season of course is very limited. A decumbent form of the arctic willow, *Salix arctica*, reaches the maximum length, and the thickest specimen with a diameter of hardly 2 cm. showed about fifty annual rings. A special feature is the rapid development of leaves and flowers, since most species flower and ripen their fruit in the course of one month, although doubtless many species do not develop ripe seeds every year.

There is but little insect life in these high arctic regions, hence the majority of plants must rely on self or wind pollination. A number of flowers are insect pollinated, however, and WULFF observed different kinds of flies, a butterfly, and some moths visiting flowers.

In his diary WULFF says that the so-called "Fjaeldmark" (WARMING) or fell-field is the only plant formation present, but his

[2] RAUNKIAER, Der arktiske og antarktiske Chamaefytklima. Biolog. Studier tilegn. Eug. Warming. Köbenhavn. 1911.

definition of this term is rather vague. WULFF's opinion seems to be explained partly by the fact that his note was written early in the season, when the snow cover was only partly removed, and only the most hardy plants, those of the fell-field, exposed. If "fell-field" be defined as an arctic (and alpine) plant formation where the individual plants are so scattered that there is bare soil between them, and consequently no room competition, then it is doubtless the dominant formation in North Greenland.

Besides this fell-field, other formations are found on especially favored places, but without exception they are of very limited extent. On a few places manured by the excrements of mammals and birds, herbaceous mats with dense vegetation exist, with *Alopecurus alpinus*, *Puccinellia angustata*, and *Poa* spp. as dominant species.

Another formation is found in the many small bogs. The characteristic species of this formation are *Eriophora*, *Arctogrostis*, *Juncus biglumis*, *Saxifraga stellaris comosa*, *Pleuropogon sabinei*, *Carex aquatilis stans*, *Eutrema Edwardsii*, etc. The shore vegetation is very poorly developed. *Puccinellia phyryganodes* and *Cochlearia officinalis groenlandica* are the only real shore species. No continuous heath is present. The heath dwarf shrubs (*Cassiope tetragona* and *Dryas integrifolia*) occur only as scattered individuals.

II

Following this short survey of the plant life of the north coast of Greenland, it seems appropriate to make a few remarks on the plant geography of Greenland north of 76°N., confining them to higher plants.

At present we know with certainty 125 species from this region, all confined to the coastal region, as the inner part of the country is covered by inland ice. Of these 125 species, most are of wide distribution in arctic regions: 85 species (or 68 per cent) are circumpolar, and 31 (or 24.8 per cent) are probably of western origin, as they are more or less common in arctic and subarctic North America, while most of them are absent from arctic Europe, although fourteen are found on the arctic islands north of Europe (Spitzbergen and Nova Zembla). Only six species are of eastern origin, that is, absent from arctic North America. The remaining three species are said to be confined to Greenland, but as two of them (*Braya Thorild-Wulffii*

and *Taraxacum arctogenum*) are recently discovered species closely allied to other better known species which are widely distributed in arctic countries, it is probable that they may yet be found in arctic North America. The third, *Lychnis* (*Melandryum*) *triflora*, is a well defined species which is common over a large part of Greenland. It would be strange if this species did not occur elsewhere in arctic America, and quite recently I have found that a plant from the delta of the MacKenzie River, *L. Dawsonii*, is a form of *L. triflora*. Altogether it seems that the three endemic species really ought to be referred to the group of western origin, as it is also less probable that a recent flora like that of North Greenland had any endemic species.

In the writer's opinion most of the arctic species are older than the ice age, which accounts for their presence both in North America and Eurasia. During preglacial times they occupied the polar regions but were forced southward by the advancing ice sheet, reaching much lower latitudes in both hemispheres. When the climate moderated and the ice retreated, the plants returned northward and reached the area occupied at present. It is quite possible that some of them may have survived the ice age in the arctic, but hardly as far north as North Greenland. Admitting this, it seems safe to say that the main part of the Greenland flora must have immigrated from other countries, and for North Greenland the only probable route was from Ellesmere Land, crossing the narrow Smith Sound to Inglefield Land on the Greenland coast at about 79°N. This immigration must have been easier during the postglacial epoch, when the climate was somewhat warmer than at present, and several species which now are found in Greenland only south of 76°N. may have come over at that time.

The same immigration route as that of the western species is probable for all the circumpolar species which did not survive in Greenland itself, as it is more natural to suppose that they immigrated to Greenland from America rather than from Europe. This means that, so far as North Greenland is concerned, only 6 of the 125 species reached there from arctic Europe. Thus the flora of North Greenland is almost entirely American from the phytogeographic point of view.

BOTANIC GARDEN
COPENHAGEN, DENMARK

TERMINOLOGY OF THE UREDINALES[1]

J. C. Arthur

As the knowledge of the rusts developed to the stage where more than one spore-form was recognized as belonging to a species, it became advantageous to employ generalized terms. For this reason the term teleutospore met with ready acceptance. It signified the last spore-form in the series, the sorus in which such spores were formed being called a teleutosorus. The serial position of other kinds of spores was not so readily apparent. Consequently no important attempt was made to extend this method of naming the several classes of spores, but instead, generic names were brought into use, such as uredospore and aecidiospore. It required no explanation that spores from an *Aecidium* were to be called aecidiospores, but what about spores from a *Peridermium* or a *Caeoma?* Logically they should be called respectively peridermiospores and caeomospores. In this way there came into use terms to cover nearly as many kinds of spores as there were generic names recognized, even going so far as to infringe upon the domain of the teleutospore with the term pucciniospore.

The reaction to this multifarious terminology arose from the recognition that many apparently diverse structures possessed a general similarity to the best known forms of *Aecidium*, both in form and function, and so the term aecidiospore was often made to cover nearly all catenulate spores borne in a peridium. When the peridium was absent they were usually called caeomospores; and stylosporic forms with or without a peridium were generally called uredospores. With this reduction of terms came the growing impression that the first two terms covered a primary form of spore, and that uredospores were a secondary form, sometimes considered as essentially conidia, leaving the term teleutospore to designate a third or final form.

[1] Contribution from the Purdue University Agricultural Experiment Station.

Presented before the Botanical Society of America at the Washington meeting, December 29, 1924.

This terminology worked fairly well with many of the most common and familiar genera, but had to be stretched to apply to the catenulate, verrucose spores without a peridium in the genus *Coleosporium*, and served very poorly in less familiar genera, such as *Kuehneola*, *Pucciniosira*, etc.

Thus the matter stood when in 1905 the writer[2] proposed new terms to replace a multiplicity of old terms, and more clearly to bring out homologies in the different stages in the life histories of the rusts. Instead of the prevailing terms which were mostly derived from generic names, the four terms: pycnium (from πυκνός, solid or compact), aecium (from αἰκία, an injury), uredinium (from *uredo*, a blight or blast), and telium (from τέλειος or τέλεος, complete or perfect), were designed to cover the different sorts of sori in every full spored, long cycle rust. The names of the spores were derived in all cases from the sori bearing them, without regard to form, surface markings, or accessories, and were respectively pycniospores, aeciospores, urediniospores, and teliospores. That these terms have proved serviceable is evident from the increasing number of mycologists who employ them.

It may be that the reason why others do not use the new terms, aside from natural inertia or undue conservatism, is the belief held by some that the terms spermogonium, aecidium, uredosorus, and teliosorus have come to have such definite application and to convey such clear concepts that there is no need of a new set of terms. In fact, to them a new set of terms really makes a difficult situation still more confusing. Even if we grant that such is the case, which is much to be doubted, yet the cumbersome form of the old names and their lack of uniformity fail to commend them.

In order to show what concepts underlie the new terminology, as well as its application, the following explanation is given. First let it be borne in mind that the new terms do not merely replace the older ones, but that they stand upon a distinctly different basis. In the first place, the terms primarily apply to the sorus, and not, as with the old terms, chiefly to the spores and their accessories. While this was the intent when the terms were first announced, yet only

[2] ARTHUR, J. C., Terminology of the spore-structures in the Uredinales. BOT. GAZ. 39:219. 1905.

within a few years have facts been available to make possible a full demonstration of the correctness of this position. Very little was known regarding the origin and intimate structure of the several forms of sori in 1905, most of the knowledge being derived from the studies of SAPPIN-TROUFFY, BLACKMAN, and CHRISTMAN, who were chiefly interested in the behavior of the nucleus. The work of a gradually increasing number of cytologists during the intervening two decades now justifies the statement that the four kinds of sori are built upon essentially the same plan. In brief, each sorus arises from a primordium, which differentiates a hymenial layer that produces spores from its upper surface. This is equally true of a pycnium or a telium, of an aecium, whether in the form of the simplest *Caeoma* or the most complex *Aecidium*, and of a uredinium, whether conidial in appearance or provided with a peridium and catenulate spores. In each of the four kinds of sori there may be more or less highly developed accessories, such as pseudoparenchyma, buffer cells, paraphyses, peridium, etc., partly evanescent and partly permanent. This essential similarity in the fundamental structure of the four kinds of sori is reflected in the similarity of the new names applied to them.

All rusts, whatever their appearance or diversity of spore-forms, pass through a two-phase life cycle: the gametophytic phase with usually uninucleate mycelium, and the sporophytic phase with usually binucleate mycelium. Every species of rust having the ancestral, long cycle development without exception terminates the first or gametophytic phase with a sorus, the aecium, in which cell fusion takes place, giving rise to binucleate spores, while the second or sporophytic phase is terminated by another sorus, the telium, in which the two nuclei of the spores, which have descended from the aecium, are at maturity fused into one. The first, or gametophytic phase, bears another form of sorus, the pycnium, if not lost in retrograde development, which in the dim ancestral uredinalean past may have been a male organ of reproduction, but now is functionless. It is uninucleate throughout. The second, or sporophytic phase, bears still another form of sorus, if not lost in retrograde development, the uredinium, which is of a repeating or conidial nature. It is binucleate throughout. To recapitulate: every long cycle rust, without excep-

tion, terminates its first phase of growth with an aecium, and its second phase with a telium, and to the first phase may or may not be added a pycnium, while to the second phase may or may not be added a uredinium. There are no exceptions to this general statement, except such as are due to extreme simplification or are to be considered pathogenic or abnormal.

When the two essential kinds of sori to be found in every long cycle rust, the aecium and telium, are telescoped into one, a short cycle rust is produced, with the sporophytic mycelium omitted. In the short cycle rust the first, or gametophytic phase, ends as it does in long cycle forms with fusion of cells, while the second or sporophytic phase, which is very short, ends when the two nuclei of the resulting spores fuse as these spores reach maturity. In consideration of this combined action the sorus may be called an aeciotelium. Sometimes there are pycnia with a short cycle rust, but never uredinia.

The two preceding paragraphs have been devoted to a brief elementary statement of the course of development among the rusts. All rusts of every sort are thus seen to have a two-phase development, whether long cycle with two forms of mycelium, and two to four forms of sori, in which aecia and telia are always present, or short cycle with one form of mycelium, and one or two forms of sori, aeciotelia always being present. This simple statement should be born in mind in trying to determine the application of the new terminology.

In 1905, in the preface of an important paper, HARPER[3] stated the grounds on which comparative morphology and the use of terms should proceed, as follows:

> Great confusion has arisen in the morphology of the fungi and algae from allowing considerations of functional equivalence or difference to mingle with and modify the conceptions of what should be a strictly phylogenetic morphology. If there can be agreement that the various developmental stages and fruit forms of the fungi and algae shall be classified and named in accordance with what can be determined as to their phylogeny, a number of disputed questions will disappear.

[3] HARPER, R. A., Sexual reproduction and the organization of the nucleus in certain mildews. Carnegie Inst. Wash. Publ. no. 37. 1905.

Two decades have passed since these statements were made, and before me lies a recent letter from HARPER, from which I have the privilege to quote, in which he says:

> It is the great outstanding achievement which revolutionized comparative morphology that we have come to realize that structures should be named not according to their function, but according to their morphological and phylogenetic connections.

Probably no one is likely to dispute this reiterated statement of a fundamental doctrine of the phylogenetic basis of modern morphology, certainly not the writer. The difficulty arises in the application.

The present state of knowledge indicates that in the rusts there are four kinds of sori, arising at successive intervals in the life cycle of every species having the ancestral, full spored cycle of development, all possessing a certain unity of structure, but differing in histological details, and each having its independent phylogenetic history. When a retrograde change has taken place in the historical development of a species, one or more forms of sori may be omitted from the cycle, going so far as to leave only aecia and telia in long cycle species and aeciotelia in short cycle species. Beside the definite consecutive positions in the life history held by the four sorts of sori, each has its distinctive fundamental structure, determined by the nuclear behavior. There is no gross structural character that belongs to one kind of sorus rather than to another, although certain forms are met with so frequently as to seem characteristic. The true nature of a sorus depends upon its phylogenetic position in the individual cycle and upon its nuclear structure.

It would be illuminating to take up a number of representative species and contrast the application of the old and new terms, but it seems scarcely necessary. If the emphasis in thinking of the rusts is placed upon the mycelial body and the fruit forms or sori which it bears in unvarying order, instead of upon the spore forms and their accessories, there should be no difficulty in apprehending the simplicity of the new terms and their suitableness for every possible situation, whatever bewildering likeness the spores and their accessories may suggest.

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BRIEFER ARTICLES

THE MITOGENETIC RAYS

(WITH ONE FIGURE)

In a recent paper[1] I reported on experiments which have demonstrated conclusively the possibility of the induction of mitoses in onion tips from other similar root tips over a distance up to 2 mm. If a root tip, occupying a horizontal position, be placed at the side surface of another vertical root tip for about three hours, a narrow median area of the "exposed" side of the latter, measuring approximately 70 μ in width, shows a con-

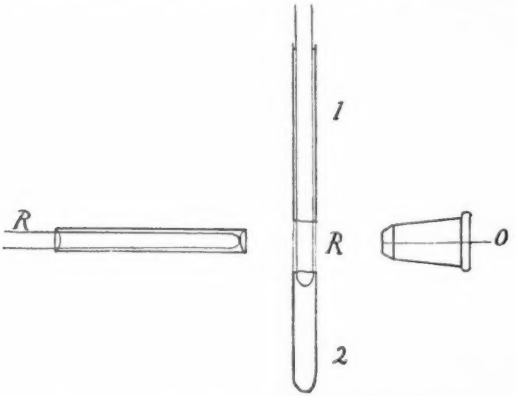

FIG. 1.—Arrangement of experiment with induction through air; both roots (*R*) placed in capillary tubes filled with water; vertical tube consists of two parts (1 and 2) between which root is covered only by a capillary water layer and is exposed to induction; *O*, horizontal microscope for controlling exactitude of position and growth of roots.

siderable increase (50 per cent and more) in the number of mitoses in comparison with the opposite side. Previous investigations, covering a period of many years, have shown that in "unexposed" root tips the difference in the number of mitoses on the "right" and "left" side in longitudinal sections exceptionally reaches 20 per cent, and alternates regularly.

The present paper reports other new facts concerning this peculiar

[1] Archiv. Mikr. Anat. Entwick. Roux. vol. 100. 1923.

mitogenetic factor, confirming the existence of a specific "mitogenetic" radiation, and giving some idea of its nature. The chief conclusions of the investigations, done with the collaboration of W. RAWIN, N. GURWITCH, and L. GURWITCH, are as follows.

1. Heteroinduction from a *Helianthus* root tip to an onion root is possible (RAWIN).

2. The induction is effected through water and through air as well (fig. 1).

3. The induction is effected, without visible decrease of intensity, over distances up to 38 mm. (maximal tested distance).

4. The interposition of a glass layer (cover slip) reduces, but does not totally suspend the effect of the induction. A glass plate of about 30 μ thickness seems not to reduce the action noticeably.

5. The interposition of a thin layer of plant tissue (onion skin, which can easily be peeled from the external surface of the layers of the bulb),

TABLE I

The action of induction is expressed in percentage of predominance of the inducted side in comparison with the non-inducted side:

Induction	Percentage
1. Simple, onion root tip on onion root tip	2, (20, 23, 60, 27, 50, 26), 0[2]
2. Through onion skin	20, 26, 16, 25, 18, 20, 26, 15, 18, 10, 20, 26, 24, 30, 25, 27, 29, 24, 15
3. Through a 30 μ wide slit	4, 0, (50, 24), 6, 2

which is highly and regularly permeable to light rays, causes a considerable dispersion of the ray beam of the mitogenetic factor (table I). Whereas normally only 6–7 central sections show the effect of induction, under the conditions mentioned this is found in approximately twenty sections of 10 μ, of course with a correspondingly decreased intensity. In view of the fact that a medium, transparent for light rays, causes a kind of dispersion of the mitogenetic factor, it seems probable that, if this factor is radiant energy, its rays must have shorter waves than light rays. It was found also that crystallinic quartz is completely transparent for mitogenetic rays, but that a thin film of gelatine will completely absorb them. This fact indicates that the wave length of the rays is in the neighborhood of 2000 Angström. Induction upon onion roots occurs also from embryonic animal tissues (small pollywogs). The following experiment gives this hypothesis an additional proof.

[2] In the experiments 1 and 3 the numbers showing a distinct result of induction are placed in parenthesis.

6. In passing through a vertical 30 μ wide slit, the ray beam does not show any trace of diffraction. As is seen in the table, two central sections are affected by the induction in this case. If we take into consideration the shrinkage due to the imbedding of the root tip, this corresponds approximately to a layer 25–28 μ in thickness. The shortest light rays (of approximately 0.4 μ) under these circumstances would give a distinct diffraction, and the root (as has been pointed out under 5) certainly would be markedly influenced. Common ultraviolet rays hardly could play a rôle in this phenomenon, as they are not noticeably absorbed by water. I may add that preliminary experiments with the photographic plate have given a negative result.—ALEXANDER GURWITCH, *University of Simferopol, Russia.*

EFFECT OF LIGHTNING ON TRUNK OF PLATANUS OCCIDENTALIS

(WITH ONE FIGURE)

In the spring of 1924, a large sycamore tree in a neighbor's yard was struck by lightning. The trunk of this tree was smooth and without branches for a distance of about 20 feet. The lightning stroke did no more damage than to remove some of the outer bark, leaving well marked paths down the trunk. There was no visible tearing or splitting of the trunk or branches. With the beginning of the growing period, however, the trunk began to develop numerous buds all the way from the branches of the large crown down to the ground. The twigs developed on all sides, although not uniformly, both on the lightning paths and on the undisturbed part of the bark. Over 200 twigs developed on the trunk, as shown in fig. 1.

This event may indicate methods of inducing active growth or rejuvenation of plant tissues which have been differentiated into a condition of stability. This tree for years had produced no buds on the trunk, but as a result of the lightning stroke it was thrown into an extraordinary activity of bud development from a previously stabilized tissue. The immediate cause at present can only be surmised. The lightning may have produced minute breaks or tearing of the cells of the cambium, or the electric charge may have produced direct changes in the protoplasm of the cells, or perhaps the development of buds was due to both causes.

Rejuvenescence and the renewing of the activity of reproduction and growth are bound to become problems of primary importance in the

physiology of the future, and it would be wise to begin the observation of all probable causes of rejuvenation and dedifferentiation, in order to begin

FIG. 1.—*Platanus occidentalis* with over 200 twigs developed on trunk in one season, as result of stroke of lightning; photograph by C. K. KAO.

an attack on this interesting and important problem.—JOHN H. SCHAFFNER, *Ohio State University, Columbus, Ohio.*

CURRENT LITERATURE

NOTES FOR STUDENTS

First sugar of photosynthesis.—During the last thirty years, several English chemists and plant physiologists have put forward the theory that cane sugar is the first synthetic sugar resulting from the action of solar energy upon carbon dioxide and water. The only supporting evidence for such a hypothesis is the fact that there is a decided diurnal fluctuation in the amount of disaccharide sugar in the leaves of plants, low at night and increasingly high by day to a maximum in the afternoon, whereas the monosaccharide hexoses are fairly constant throughout the same period.

It is only fair to American plant physiologists to say that this cane sugar hypothesis has never been taken seriously on this side of the Atlantic, preference having been given always to the hypothesis that dextrose is the first sugar. It is a satisfaction, nevertheless, to have PRIESTLEY[1] reinterpret the older work of BROWN and MORRIS, and the more recent work of PARKIN, DAVIS, DAISH, and SAWYER, and reach the conclusion that the data really support the formation of hexoses as the primary photosynthetic sugars.

The difficulties involved in an explanation of the rôle of cane sugar in plants is well set forth in PRIESTLEY's discussion. He proposes a rather difficult solution of a difficult problem, namely, that cane sugar is not a storage product arising from enol formation and ultimate union of dextrose and levulose, nor does it arise directly from starch hydrolysis, enol formation, and synthesis. He prefers to believe that cane sugar is a product of intimate cellular metabolism by differentiating tissues. Thus the carbohydrate reserves, like starch or inulin, or the direct primary photosynthetic sugars, would be consumed in the active synthetic metabolism of the meristematic regions, and cane sugar would arise in some intricate way as a byproduct of this utilization of the reserves. Subsequently the cane sugar might be lost from the cells as the latter reach their elongation and maturation phases through vacuolation and differentiation, as possibly happens in cases where cane sugar appears in the sap flowing from decapitated vines and trees.

PRIESTLEY puts his views forward merely as a working hypothesis. Certainly the subject needs much careful investigation, and we need more adequate methods of recognition of the various sugars in mixtures, and particularly of distinguishing disaccharides from one another, and from glucosides. One would ultimately like to have an explanation which fits adequately to the main sources of cane sugar, the sugar beet and sugar cane.—C. A. SHULL.

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[1] PRIESTLEY, J. H., The first sugar photosynthesis and the rôle of cane sugar in the plant. New Phytol. **23**: 255–265. 1924.

Hydrogen-ion concentration and vegetation.—An effort to relate vegetation more exactly to soil acidity is seen in several recent studies that follow somewhat similar lines to those developed by KURZ.[2]

STRØM[3] examined numerous bodies of water in Norwegian mountains, and found their P_H values to range from 3.8 to 8.5. Typically aerated localities gave an average P_H value of 7.6, and several stagnant habitats gave an average of 4.5, showing that aeration is here the most important factor in controlling acidity. Under subarctic conditions, the majority of even stagnant localities are so well aerated that they show a neutral or only slightly acid reaction. The specific reaction of the water is regarded as a potential factor in determining the character of the vegetation, and more especially that of the algal flora.

Dealing more particularly with upland vegetation, CHODAT[4] has reported a detailed study of the soils of many of the plant associations of eastern France and Switzerland. He lays emphasis on his conclusion that each plant seems to grow in soils having a certain obtainable range of P_H values, and that this amplitude of accommodation to the soil reaction, expressed in P_H values, should replace such terms as calcifuge, calcicole, etc. Plant associations on soils of similar P_H values he regards as homologous, and several such groups are distinguished.

BRAUN-BLANQUET[5] has determined the H-ion concentration of the soils of many of the garique associations of southern France, and finds that it varies little from the neutral (P_H 7). While he regards the acidity of the soil, its calcium carbonate content, and its colloidal properties as important factors influencing the distribution of plants, the first seems inadequate to serve as a means of classifying the plant associations designated as garique.

In a more general discussion, SALISBURY[6] emphasizes the facts that the causes of soil acidity are various, that the reaction of an undisturbed soil is fairly constant throughout the year, and that the soil reaction is only one of many factors which determine the nature of the plant covering. He plots frequency curves with the P_H values as abscissae and the number of localities as ordinates for several plants. These curves for the different species do not ex-

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[2] KURZ, H., Hydrogen-ion in relation to ecological factors. BOT. GAZ. **76**:1–29. 1923.

[3] STRØM, K. M., P_H values in Norwegian mountains, and their bearings upon the classification of freshwater localities. A reconnaissance. Nyt. Mag. Naturvidensk. **62**:237–244. 1925.

[4] CHODAT, F., La concentration en ions hydrogène du sol et son importance pour la constitution des formations végétales. Université de Genève, Thèse no. 748. pp. 115. 1924.

[5] BRAUN-BLANQUET, J., Études sur la végétation méditerranéene. III. Concentration en ions H et calcimétrie du sol de quelques associations de la garigue languedocienne. Bull. Soc. Bot. France **71**:639–647; 879–891. 1924.

[6] SALISBURY, E. J., The incidence of species in relation to soil reaction. Jour. Ecol. **13**:149–160. 1925.

hibit modes corresponding to the same P_H value as they would if they were determined by the frequency of soils of a particular reaction, and some of the species exhibit a bimodal form, whereas the soil curve is monomodal. He also discusses the importance of a ratio of potassium to calcium as a factor in distribution, and concludes that the reaction of the soil as expressed in P_H values is much more significant, being one of several important factors that govern the distribution of plant species under natural conditions.—GEO. D. FULLER.

Specificity of enzymes.—The specificity of enzyme action among the carbohydrate splitting enzymes has been much studied, and such action clearly demonstrated, but it has not been so clear that the proteolytic enzymes were similarly specific for the proteins which they usually hydrolyze. BLAGOVESCHENSKI[7] has investigated the action of proteases on plant globulins, using globulins from *Cannabis sativa*, *Brassica Rapa*, *Lupinus luteus*, *Phaseolus Mungo*, *Dolichos melanophthalmus*, *Hibiscus esculentus*, and *Lathyrus sinensis*. Using the protease derived from some one plant, its rate of reaction on the globulin from the same species, and on globulins from the other species, was compared by following the changes in amino-nitrogen during the reaction. Every protease was found to split the globulin of its own species more actively than those from any of the other species.

A study of the specific conditions of enzyme action of leaves has been made by BLAGOVESCHENSKI[8] and his coworkers, SOSSIEDOV[8], and BIELOZERSKI.[9] For the leaf invertases it has been found that each species of plant has a different optimal hydrogen-ion concentration, and that variation in percentage of hydrolysis with change in P_H is of a very specific nature. Thus in the leaves of *Vitis vinifera*, the optimum P_H for its invertase is 5.0, in *Gossypium herbaceum* 5.6, in *Glycyrrhiza glabra* 4.5, and in *Pyrus communis* 6.2. Fourteen species are recorded, each showing specific differences in the hydrogen-ion concentration relations of its own invertase. The peptases of different plants likewise have specific optimal hydrogen-ion concentrations for their action upon peptone. The optimum values for several species are given. For *Pyrus Malus* 4.5, *P. communis* 5.8, *Juglans fallax* 6.7, *Syringa vulgaris* 7.7, *Ungernia Severzovii* 8.0.

These investigations are of interest from the standpoint of comparative physiology, and emphasize the specific nature of protoplasmic products. Just how far one may go in applying these results to the problem of origin of species remains to be seen. BLAGOVESCHENSKI suggests that the origin of systematic species seems to be reduced to a purely chemical problem of the evolution of the proteins and other chemical bodies in the protoplasm, such chemical evolution expressing itself in external form, as well as in internal physiological character

[7] BLAGOVESCHENSKI, A. V., On the specific action of plant proteases. Biochem. Jour. **18**:795–799. 1924.

[8] BLAGOVESCHENSKI A. V., and SOSSIEDOV, N. I., The specific conditions of action of leaf invertases. Biochem. Jour. **19**:350–354. 1925.

[9] BLAGOVESCHENSKI, A. V., and BIELOZERSKI, A. N., The specific conditions of action of leaf peptases. Biochem. Jour. **19**:355–356. 1925.

and behavior. This is probably putting the case too strongly, but it does seem certain that physiological behavior and differentiation is sensibly specific, and that no one can draw very wide conclusions from the study of one, or even several species of plants.—C. A. SHULL.

Taxonomic notes.—YAMADA[10] has reported on collections of marine Chlorophyceae made on the Island of Formosa. The 33 species listed belong to 18 genera, distributed among 7 families. Four new species are described in the following genera: *Dictyosphaeria*, *Rhipidiphyllum*, *Cladophora*, and *Chlorodesmis*.

JOHNSTON[11] has contributed an investigation of the North American species of *Cryptantha* as the fourth paper in the studies of Boraginaceae. It is a very full record of all available material and bibliography. The general discussion includes the history, gross morphology, and generic relations of the genus. The author recognizes 57 species, grouped in 15 series, only 2 species being described as new. It is noteworthy that 35 of the species are credited to GREENE.

NAKAI[12] has published the results of a critical study of certain Japanese ferns. He considers 31 species in 8 genera, 5 of the genera represented each by a single species. The large genera are *Woodwardia*, with 11 species, one of which is new; *Polystichum*, with 10 species and 10 varieties; and *Pteridium*, with 5 species and 5 varieties.

MACBRIDE[13] has published an account of South American plants, mostly from the Captain Marshall Field expedition to Peru in 1922 and 1923. He includes 14 genera, represented by 29 species, 8 of which are new. Among them *Psoralea* is represented by 6 species, 4 of which are new. The same publication includes 2 new species of *Canavalia* by PIPER, and 2 new species of *Tithymalus* (Euphorbiaceae) by MILLSPAUGH.

PIPER[14] has undertaken to clarify the confusion that has existed in reference to the genus *Canavalia* (Leguminosae). As a result of the study of American species, the genus *Wenderothia* is restored, including 12 species, one of which is new; and *Canavalia* includes 26 species, 13 of which are new.—J. M. C.

Haustoria of dodder.—In a very detailed study, ZENDER[15] has examined the manner in which *Cuscuta europaea* penetrates its hosts, using material from

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[10] YAMADA, YUKIO, Studien über die Meeresalgen von der Insel Formosa. Bot. Mag. Tokyo **39**:77–95. *figs. 5.* 1925.

[11] JOHNSTON, I. M., The North American species of *Cryptantha*. Contrib. Gray Herb. N.S. no. 74. pp. 114. 1925.

[12] NAKAI, T., Critical notes of Japanese ferns with special references to the allied species. Bot. Mag. Tokyo **39**:101–121. 1925.

[13] MACBRIDE, J. F., South American plants. Field Mus. Nat. Hist. Publ. 231. Bot. Series **4**:79–95. 1925.

[14] PIPER, C. V., The American species of *Canavalia* and *Wenderothia*. Contrib. U.S. Nat. Herb. **20**:555–588. 1925.

[15] ZENDER, J., Les Haustoriums de la *Cuscuta* et les réactions de l'hôte. Thèse no. 757, Université de Genève. pp. 81. 1924.

families extending from the Pteridophytes to the Compositae. Many variations in the haustoria are described and figured, but the only reaction on the part of the host is the development of some little wound tissue in a few plants such as *Rubus idaeus* and *Chaerophyllum silvestre*. Active chemical metabolism is indicated by the enlarged nuclei of the haustoria. The disorganization of the host tissues is shown[16] to be similar to that caused by parasitic fungi. Special attention is given to the behavior of haustoria in the xylem and phloem regions. In the former the conductive elements of the parasite apply themselves very closely to those of the host, fitting accurately into the pores and about the thickenings of the tracheae. They are apparently readily able to absorb water and dissolved mineral salts very soon after their entrance. Approaching the phloem the haustoria seem stimulated to greater extension, and send out digitately branched processes which enter the sieve tubes and companion cells, indicating that their contents are used in the nutrition of the parasite.

This study seems to be carefully made, well illustrated by drawings, and of a nature that makes a substantial advance in our knowledge of the subject.—GEO. D. FULLER.

Botany and weeds.—A recent publication[17] demonstrates well the advantages of attacking an economic problem by scientific methods. *Cyperus rotundus* is one of the most troublesome weeds of moist tropical soils. In India, where it is known as the "lavala weed," it reduces the annual yield of fertile tracts 25–30 per cent. Its multiplication by seeds, tubers, and rhizomes have made it particularly difficult of eradication.

A committee appointed by the Director of Agriculture of India, and charged with devising methods of control, decided to proceed by making a thorough botanical study of the plant rather than by the usual method of large scale experiments in the field. The results as expressed in this bulletin include a careful taxonomic, anatomical, and ecological study of all phases of its life history, with particular attention to its various methods of propagation. This includes many experiments on seed germination and planting of tubers, all yielding interesting results, that are reported in detail and are important in leading by various routes to the vulnerable point in the life history of the weed, that is, to the conditions necessary for the development of the seeds and tubers.

From these data it has been possible to formulate at once a program of eradication that will doubtless be more efficient than any indicated by field experiment alone. This consists in a combination of fallowing during the dry season and cultivation during the rainy months. The results have thus entirely justified the method of first studying the plant, and only later dealing with field practice.—GEO. D. FULLER.

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